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NUMBER 59 **DECEMBER 20, 1996**

Systematics and Evolution of Cenozoic American Turritellidae (Mollusca: Gastropoda) I: Paleocene and Eocene Coastal Plain Species Related to "*Turritella mortoni* Conrad" and "*Turritella humerosa* Conrad"

by

Warren D. Allmon

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Subscriptions to *Bulletins of American Paleontology* may be started at any time, by volume or year. Current price is US $75.00 per volume. Numbers of *Palaeontographica Americana* are priced individually, and are invoiced separately on request.

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Ithaca, New York, 14850 U.S.A.

ISSN 0078-8546
ISBN 0-87710-436-0
Library of Congress Card Number: 94-065492

Printed in the United States of America
Allen Press, Inc.
Lawrence, KS 66044 U.S.A.

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SYSTEMATICS AND EVOLUTION OF CENOZOIC AMERICAN TURRITELLIDAE (MOLLUSCA: GASTROPODA) I: PALEOCENE AND EOCENE COASTAL PLAIN SPECIES RELATED TO "*TURRITELLA MORTONI* CONRAD" AND "*TURRITELLA HUMEROSA* CONRAD"

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ABSTRACT

Gastropods of the family Turritellidae are among the most important components of macrofossil assemblages in the Paleocene and Eocene of the U.S.Gulf and Atlantic Coastal Plains, and are of considerable biostratigraphic utility, yet their phylogenetic relationships have remained obscure. This paper treats 52 of these turritellid species, focussing on those related to the common and well-known species "*Turritella mortoni* Conrad" and "*Turritella humerosa* Conrad". Of the shell characters available in these species, the early ontogeny of spiral sculpture is believed to be the most reliable homology and so the best indicator of phylogenetic relationship.

Because of the relatively high completeness of the Coastal Plain stratigraphic section, and the relative paucity of shell characters in these species, a two-step approach to phylogenetic analysis is used. Atemporal cladistic procedure, considering supraspecific turritellid taxa from other times and geographic regions, is used for analysis of relationships of species groups. Stratophenetic methods are used for analysis of relationships of species within these groups.

The genus *Turritella* Lamarck has long been recognized as a form-genus and taxonomic wastebasket, but the taxonomic diversity and subtlety of morphological difference in turritellids, at least in the U.S. Coastal Plain, have hindered development of a coherent supraspecific taxonomy. This paper represents a first attempt at such a taxonomy. Three species groups are recognized: species most closely related to *Turritella mortoni* Conrad are placed in the new genus *Palmerella*; species most closely related to *Turritella rina* Palmer are placed in the genus *Haustator* Montfort; species most closely related to *Turritella humerosa* Conrad are placed (temporarily) in "*Turritella*" *sensu lato.*

Multivariate morphometrics are used, apparently for the first time in turritellids, to discriminate species and subspecies. In part with the aid of these methods, "*Turritella mortoni* Conrad" is divided into four chronological/geographic subspecies: *Palmerella mortoni mortoni* (Conrad), *P. m. mediavia* (Bowles), *P. m. postmortoni* (Harris), and *P. m.* ssp. By similar methods, "*Turritella" praecincta* Conrad is divided into two geographic subspecies: *"Turritella" praecincta praecincta* Conrad and *"T." p. virginiensis* n. ssp.

Two species are recognized as new: *"Turritella" toulmini,* and *Palmerella stenzeli.*

ACKNOWLEDGEMENTS

I am especially grateful to D.T. Dockery, S.J. Gould, R.D. Turner, and L.W. Ward for all manner of suggestions, support, assistance and advice at various stages throughout this project. Thanks are also due to R.L. Aiello, R.C. Eng, F.C. d'Escrivan, R.M. Ross and J.R. Tegan for their patience, help and support at crucial times, to T. Rice for scanning electron microscopy, to S.A. Schellenberg and especially J.R. Tegan for assistance with morphometric analysis, to D. Campbell, W. Fallaw, C. Garvie, and V. Zullo for sharing unpublished information and to P. Gan for assistance with indexing. I owe a special debt to P.J. Morris, without whose patience, skill and computer wizardry the morphometric analyses presented here would never have been possible. Any errors or misinterpretations in these analyses are of course wholly my own.

Thanks are due J. Allen (Alexandria, La.), E. Benamy (Academy of Natural Sciences of Philadelphia), W. Blow (U.S. National Museum), M. Carman (Field Museum of Natural History), K. Boss (Museum of Comparative Zoology), C. Durden (Texas Memorial Museum), P. Hoover (Paleontological Research Institution), R. Portell (Florida Museum of Natural History), C. Smith (Geological Survey of Alabama), and R. Stanton (Texas A&M University) for making possible loans of specimens from collections under their care.

D.T. Dockery, S.J. Gould, R.S. Houbrick, and R.D. Turner read earlier drafts and made many valuable comments.

This work was supported by grants from the Geological Society of America and Sigma Xi, by funds from the Department of Earth and Planetary Sciences of Harvard University and the Department of Inverte-

brate Paleontology of the Museum of Comparative Zoology, and by a National Science Foundation Graduate Fellowship. Publication was made possible by the Trustees of the Paleontological Research Institution.

This paper is dedicated to the memory of Joe Houbrick and Wally Fallaw.

INTRODUCTION

In abundance of individuals and diversity of species, gastropods of the family Turritellidae are among the most important macrofossils in many Cretaceous and Cenozoic deposits worldwide (Allmon, 1988a). Nowhere is this more true than in Paleocene and Eocene strata exposed along the Gulf and Atlantic Coastal Plains of the United States, where turritellids are known from almost all marine units. Some beds contain virtually no macrofossils other than turritellids, varying in abundance from rare to densely packed; others contain a diverse mollusk fauna in which turritellids are of varying importance (Allmon and Dockery, 1992; Allmon and Knight, 1993). Although usually no more than one or two turritellid species are present in the same horizon, several beds contain as many as four or five. Here as elsewhere in the world, the abundance, wide geographic ranges, and relatively short stratigraphic duration of many turritellid species have led to their widespread use as guide fossils (*e.g.,* Stenzel, 1940; Sohl, 1977; Toulmin, 1969, 1977); together with ostreid and venericard bivalves, they are the among the most biostratigraphically important macrofossils in the region.

The nature of Turritellidae as a group suggests, furthermore, that it may be fertile ground for studies of considerable general evolutionary interest. Turritellids appear to be an example of prodigious taxonomic diversity but relatively little morphological disparity. Turritellid evolution has been a story of both abundant speciation and repeated development, in both time and space, of a relatively small variety of forms (Kotaka, 1978; Allmon, 1987, 1994).

In spite of this abundance, diversity and evident biostratigraphic and evolutionary importance, however, Coastal Plain turritellids are poorly understood. Although considerable attention has been given to their description and classification, attempts at phylogenetic analysis have met with only limited success, and without coherent and reliable phylogenetic hypotheses, studies of evolutionary pattern and process in this prolific group have not been possible. This paper has three principle objectives: 1) to propose a preliminary, testable phylogeny for a large group of turritellid species from the Paleocene and Eocene beds of the U.S. Gulf and Atlantic Coastal Plains, specifically those related to the common, conspicuous and well-known species *Turritella mortoni* Conrad 1830 and *T. humerosa* Conrad 1835b, which may serve as a basis for future evolutionary and biostratigraphic studies; 2) to present new formal descriptions of these taxa, most of which have not been systematically treated in more than half a century; 3) to place these species in the context of turritellids from other times and regions and begin the task of erecting a valid and useful classification and phylogeny of the entire family. Of the 69 species and subspecies in the family named from the Paleocene and Eocene of the coastal plain (excluding the genus *Mesalia*) (Allmon, 1988b), this paper treats in detail 52.

DIFFICULTIES WITH TURRITELLIDS

Phylogenetic and evolutionary analyses of turritellids are difficult for a number of reasons. Very little is known about either the ecology or non-shell characters (*e.g.,* opercular and radular form, soft-part anatomy) of living members of the family (see Allmon, 1988a; Allmon *et al.,* 1992, 1994). Therefore, in this respect, adequate comparative data do not exist for studies of fossil species. More importantly for the purposes of this paper, the simplicity of the turritellid shell limits the number of characters available for phylogenetic analysis of fossils. As noted by many authors over the years, the turritellid shell consists essentially of little more than a high-spiralled tube of roughly circular cross-section, ornamented externally by spiral cords and occasionally some minor axial sculpture. This paucity of characters has several implications:

1) Phylogenetic analysis. So few morphological characters are available in the shell of turritellids, and those available are so simple, that the possibility of homoplasy is difficult to discount for almost any proposed set of relationships based on shell characters alone. For example, although Merriam (1941) and Marwick (1957a) have placed great emphasis on growth line form as an important taxonomic character, both authors also raise the possibility that growth lines can be susceptible to homoplasy. Several workers have emphasized ontogeny of spiral sculpture, but MacNeil (in MacNeil and Dockery, 1984, pp.48–49) states that "it is difficult to imagine" that species of similar external form and sculpture are unrelated even though they differ in early sculpture. As a result of this ambiguity, other criteria usually must be used to derive phylogenetic hypotheses.

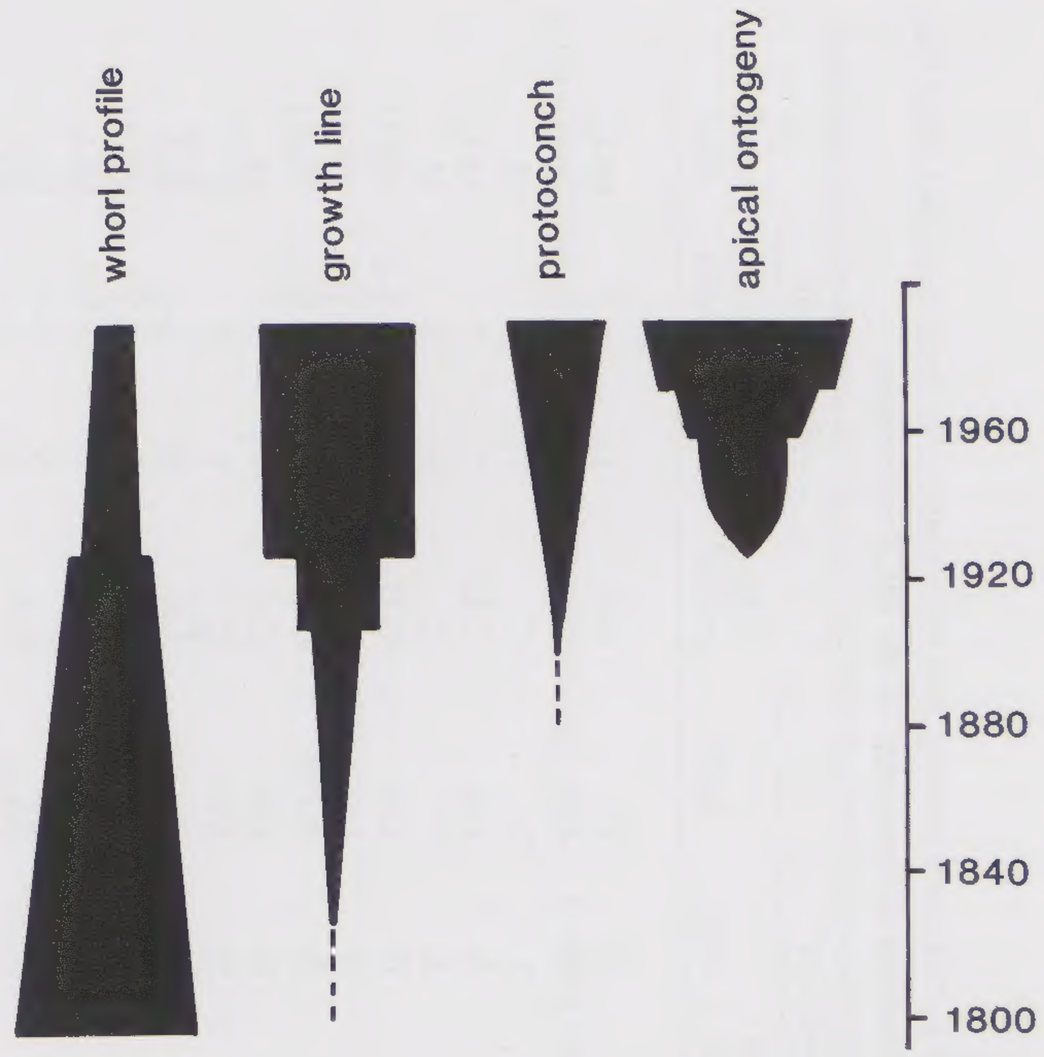
2) Definition of supraspecific taxa. With probably 2000 named species and subspecies, fossil and Recent (Allmon, unpubl. compilation), the genus *Turritella, sensu lato,* long ago ceased to be useful in the sense of facilitating data retrieval, yet efforts toward a meaningful subdivision have been hindered by lack of phylogenetic knowledge. At least 35 generic or subgeneric names have been proposed for fossil or living species

in the subfamily Turritellinae alone (see Table 1), but few have come into general use. Definition of supraspecific taxa in the group has in fact tended to depend on unstated or ill-defined taxonomic philosophy (Allmon, 1992a), and as a result no serious supraspecific evolutionary hypotheses have been proposed.

3) Biogeographic control. Without reliable phylogenetic interpretation, biogeographic history cannot be interpreted; yet biogeography can influence preliminary phylogenetic hypotheses by suggesting which species should be included in an analysis. I explore this relationship here by making use of both morphological and biogeographic data independently and together in a comparative fashion.

Given the paucity of characters in fossil turritellid shells, it could be argued that a more appropriate method of analysis for this group of animals would begin with exhaustive study of living taxa; fossil forms could then be viewed in the context of preliminary phylogenetic hypotheses on this basis. I have not proceeded in this way for two reasons. The first is that the present is not an adequate guide to the past for many aspects of turritellid biology. Not only have ecological parameters such as substrate and temperature preference possibly changed (Allmon, 1988a, 1992b; Allmon and Knight, 1993), but the former pan-Tethyan distribution of the group, like that of many cerithioid gastropods (Houbrick, 1981, 1984a; Jung, 1987), contracted in the late Cenozoic to a current center of diversity in the southwestern Pacific (see Allmon, 1992b for further discussion). Although it is probably true that data from fossils will seldom overturn a phylogenetic topology established on the basis of living taxa (Patterson, 1981), only the fossil record can document the actual course of evolutionary events in a clade's history. In a group such as Turritellidae, which clearly has so substantial a previous history, Recent taxa do not provide sufficient information to answer many important evolutionary questions.

The second reason is that one must start somewhere. Studies of living turritellids are few (*e.g.*, Allmon, 1988a; Allmon *et al.*, 1992, 1994; Lieberman *et al.*, 1993), and we know little about the biology of the great majority of species. In any study, it would of course be ideal to know the outcome at the beginning. This is especially true in systematic work, where the result is so often greatly affected by the starting point; the characters and taxa included in a systematic study, particularly of a diverse and widespread group, will often be influenced in part by the experience and background of the systematist. But where does one gain such experience? This paper discusses *some* of the turritellid species from *one* region during *one* interval of time. Adequate understanding of the phylogeny of these species, however, depends on detailed knowledge of older and younger species from elsewhere, knowledge that does not yet exist. I would like to know the morphology and distribution of all other turritellid species, but I do not. The hypotheses I propose here can therefore be no more than tentative, constrained by the very limited data that are available at present. I hope that they may serve as a basis for future systematic work in this important but neglected group of gastropods.



Text-figure 1.—Subjective estimates of the relative importance of the four principal shell characters used in the classification of the family Turritellidae since the description of the genus *Turritella* by Lamack in 1799.

HISTORY OF STUDY

The history of systematic study of the Turritellidae has been well summarized elsewhere (Merriam, 1941; Allison, 1965, 1967; Allison and Adegoke, 1969), and only the main points will be touched upon here, especially as they are relevant to the classification of Coastal Plain species. Several studies of Paleogene Coastal Plain forms have in fact contributed to the classificatory practice for other turritellids, and so the two stories are to some degree interrelated.

Classification of the family can be usefully thought of as having proceeded through three partially overlapping phases (Allison, 1967), during which more emphasis was placed on one or another of the four most conspicuous conchological characters of the turritellid shell: whorl profile, form of the growth line, ontogeny of spiral sculpture, and protoconch form (Text-figure 1).

Lamarck erected the genus *Turritella* in 1799 to contain the Recent western Pacific species *Turbo terebra*

Table 1.—Character states for supraspecific taxa in the family Turritellidae. Taxa listed include those recognized by Marwick (1957a) and all supraspecific taxa described since that time. Character state information derived from Marwick (1957a), original descriptions and illustrations, and observations of specimens in the MCZ collections.

Taxon[1]	*strat. range*	*apical sculpture formula*	*growth line*[2]					*whorl profile*[3]	*protoconch*		*shell size*[5]
			basal sinus	*lateral type*	*sinus depth*	*apex*	*angle*		*diam-eter*[4]	*no. whorls*	
Subfamily Turritellinae											
Archimediella Sacco, 1895	Oligocene	C2 B1 A3	3	3	S	C	P	C-J	L	1.5	M-L
A. (*Torculoidella*) Sacco, 1895	Pliocene	?	3	3–4	S	B	P	D-J	?	?	M-L
Callostracum Smith, 1909	Recent	?	?	?	?	?	?	C	?	?	M
Coeloconica Eames, 1957	Eocene	?	?	2?	M	A	OR	C-D	?	?	M-L
Colposigma Finlay & Marwick, 1937	Danian	C2 B1 A3	3	1	M	A	?	C	S	3	M
Colpospira Donald, 1900	Eocene-Rec.	d C1 b3 A2	2	2	D	B	OR	C-D-J	L	1.5–2	VS-M
C. (*Acutospira*) Kotaka, 1959	Eocene	C1 B3 A2/C1 A2	6?	2	D	B	OR	X-W	L	1.5–2	VS-M
C. (*Platycolpus*) Donald, 1900	Recent	C3 B1 A2/C2 B1 A3	2	2	M	B	P-OR	C-D	L	1.5–2	VS-M
Colpospirella Powell, 1951	Recent	?	3	4	M	B	OR	C-J	?	?	M
Costacolpus Marwick, 1966	U. Cretaceous	?	1	4	S	B	VP	C	?	?	S
Cristispira Allison, 1965	M.-U. Eocene	d C2 B1 a3	4?	1	M	A	P	J-V	S	3–4	M-L
Ctenocolpus Iredale, 1924	Miocene-Rec.	C1 B A	2	3	M	B	P	J-U	L	1.5	VS-M
Gazameda Iredale, 1924	U. Mio.-Rec.	c2 B1 a3	4	2	M	B-C	P	D-J	L	1.5–2	M-L
Hataiella Kotaka, 1959	Olig.-Mio.	C1 B2 a3	3	1	M	B	OR	C	S	2–3	M
Haustator Montfort, 1810	Eo.-Rec.	C1 B2 a3	4	2	M	B-C	P-OR	J	S-L	2–3	S-L
H. (*Kurosioia*) Kotaka, 1959	Pleist.	C1 B2 A3	4	1	M	B	P	C-D	S	3–5	S-M
Idaella Kotaka, 1959	Miocene	C2 B1 A3	3	1	M	A-B	OR	C-D	S	2	M
Maoricolpus Finlay, 1926	Olig.-Rec.	C2 B1 A3	3	1	M	B-C	P	J	S	2.5–4	S-VL
Neohaustator Ida, 1952	Plio.-Rec.	C1 B2 a3	3	1	M	A-B	P-OR	C-J	?	?	M
Nipponocolpus Kotaka, 1959	Recent	?	?	1?	M?	A	OR	C	?	?	L
Peyrotia Cossmann, 1912	Miocene	?	3	4	M	B	P	C-J	?	?	M-L
Reymentella Adegoke, 1977	U. ? Paleocene	d c b a r	3?	2?	S?	B	P-OR	L-H	S	2.5–3	S
Sechuritella Olsson, 1944	U. Cretaceous	?	?	4	M?	B	VP	D-X	?	?	?
Spirocolpus Finlay, 1926	Eocene	C1 B2 A3	3	3	D	B	OR-OP	C-J	S	2–3	M
Torcula Gray, 1847	U. Eoc.-Rec.	C1 B2 a3	4	1	M	B	P	U	L	1–2	M
T. (*Bactrospira*) Cossmann, 1912	Pliocene	?	4	4	M	B	P	J-U	?	?	M
T. (*Eurytorus*) Gardner, 1947	Miocene	?	?	?	?	?	?	J-U	?	?	M
Torquesia Douvillé, 1929	Cret.-Eocene?	C1 B2 A3?	3	2	M	A	P-OR	X-Q	S	2–3	M-L
Tropicolpus Marwick, 1931	U. Oligocene	C1 B1 a2	6	2	M	B-C	P	X-U	?	1–3	L
T. (*Amplicolpus*) Marwick, 1971	U. Pal.-L. Mio.	C1 B1 a2	?	2?	M	A-B	P	X-U	?	2–2.5	L-VL
Turritella Lamarck, 1799	?	C4 t3 B1 A2	2	4	S	B	P-VP	C-J	S?	?	L
Wyatella Adegoke, 1967	M.-U. Eocene	d C1 B1	?	1	M	A	OR	X-Y	?	?	M
Zeacolpus Finlay, 1926	Plio.-Rec.	C2 B1 A3	3	2	M	B-C	P	D-J	?	?	M
Z. (*Leptocolpus*) Finlay & Marwick, 1937	L. Pal.	?	3	1	S	B	P	D-J	?	?	M
Z. (*Stiracolpus*) Finlay, 1926	Plio.-Rec.	C2 B1 A2/C2 B1 A3	3	1	M	B	P	C-V	?	?	M
Subfamily Protominae Marwick, 1957a											
Protoma Baird, 1870	Mio.-Rec.	C2 B1 A3	5	1	M	A	P	J	?	?	M
P. (*Protomella*) Thiele, 1931	Recent	?	5	?	M	A	P	J	?	?	M

Table 1.—Continued.

Taxon[1]	strat. range	apical sculpture formula	growth line[2]					whorl profile[3]	protoconch		shell size[5]
			basal sinus	lateral type	sinus depth	apex	angle		diam-eter[4]	no. whorls	
Subfamily Pareorinae Finlay and Marwick, 1937											
Craginia Stephenson, 1952	U. Cretacous	?	?	3	M	A	P	C-J	?	?	M
Mesalia Gray, 1847	Pal.-Rec.	C1 B1 a2	1	3	S	B	P-OR	C	S	2–3	M
Motyris Eames, 1952	Eocene	?	?	?	S	?	?	C	?	?	M
Neodiastoma Cotton, 1932	Recent	?	1	3	S	B	OR	C	?	?	M
Pareora Marwick, 1931	Oligocene	C2 B1 A3	1	1	M	A	OR	C	S	>3?	VS
Sigmesalia Finlay & Marwick, 1937	Eocene	?	1	4	M	B	OR	C	?	?	M
Tachyrinchella Titova, 1994b	Oligocene	C1 B1 a3?	?	4	M	A	P	C	?	?	M
Tachyrhynchus Mörch, 1868	Recent	C2 B1 a3	1	4	S	B	OR	C	?	?	S
Woodsalia Olsson, 1929	Eocene	?	?	?	?	?	?	J	?	?	M-L
Zaria Gray, 1847	Recent	C1 B2 a3	1	4	M	B	VP	C-J	?	?	VL
Subfamily Turritellopsinae Marwick, 1957a											
Glyptozaria Iredale, 1924	Recent	C1 B1	1	4	S	?	?	C	?	1.5	VS
Kimberia Cotton and Woods, 1935	Recent	C2 B1 A3	?	?	?	?	?	C	?	3–4	VS
Orectospira Dall, 1925	Recent	?	?	?	?	?	?	H	?	?	S-M
Turritellopsis Sars, 1878	Recent	C1 B1 A2	?	?	?	?	?	C	?	?	VS-S
Subfamily Vermiculariinae											
Vermicularia Lamarck, 1799	Plio.-Rec.	c1 b2 a3	1	4	M	B	P-OR	D-J	S	>3?	M-L

[1] Supraspecific taxa as listed by Marwick (1957a) or as described since then.
[2] Growth line traces as represented in Text-figure 10.
[3] Whorl profiles as represented in Text-figure 13.
[4] Protoconch diameter (P1 + P2): Small (S) = <~250 μm; Large (L) = >~250 μm.
[5] Size (maximum observed shell length) classification follows that of Marwick (1971): Very Large (VL) = >100 mm; Large (L) = 50–100 mm; Medium (M) = 20–50 mm; Small (S) = 10–20 mm; Very Small (VS) = <10 mm.

Linnaeus, 1758. Lamarck's generic description (1799, p.74) reads in full as follows:

> Coq. turriculée; l'ouverture arrondie, entiere, mais ayant un sinus au bord droit.
>
> (Shell turriculate; aperture round, entire, possessing a sinus at the outer edge.)

Between 1810 and 1912 several generic names were proposed for species similar to *T. terebra*; as Allison (1967) has pointed out, these names were based largely on differences in whorl profile, external sculpture of adult whorls, and overall shell form. These include *Haustator* Montfort, 1810, *Smithia* Maltzan, 1883, *Archimediella* Sacco, 1895, *Torculoidella* Sacco, 1895, *Altavillia* de Gregorio, 1908, *Callostracum* Smith, 1909, *Bactrospira* Cossmann, 1912 and *Peyrotia* Cossmann, 1912. As Allison has also noted, however, several other generic names were proposed during this period based on more detailed morphological criteria, especially form of the growth line. These include *Proto* Defrance *in* Blainville, 1824, *Tachyrhynchus* Mörch, 1868, *Protoma* Baird, 1870, *Turritellopsis* Sars, 1878, and *Colpospira* Donald, 1900. In addition, Gray (1847) described two genera in the group (*Torcula* and *Zaria*), but without descriptive comments of any kind.

Cossmann (1912) reviewed all previous work, and recommended that the form of the growth line be employed, together with whorl profile and external (adult) sculpture, in classification of the group. As pointed out by Merriam (1941, p.30), Cossmann was the first to attempt explicit definitions of what characters should be used to delimit supraspecific taxa in the family. Yet, although he suggested the use of growth line form, he did not use this character in his classification. Guillaume (1924) criticized Cossmann on this point, noting that forms with similar growth lines had been placed by Cossmann in different taxa, whereas forms with very different growth lines had been placed in the same taxa, largely on the basis of whorl profile and overall shell form. Guillaume arranged European Tertiary species into five groups based exclusively on growth line form. Dollfus (1926) criticized this reliance on a single character.

In the 1920's, a number of New Zealand workers (Iredale, 1924, 1925; Finlay, 1926, 1930; Marwick, 1931; Finlay and Marwick, 1937) began to emphasize the importance of the ontogeny of spiral sculpture, *i.e.*, the order of appearance and change in relative strengths of the spiral ribs, particularly on the earliest whorls, in grouping fossil and Recent species into supraspecific taxa. These authors described additional supraspecific taxa, relying mainly on spiral ontogeny, but also with consideration of growth line, whorl profile and protoconch and opercular form. Taxa introduced by these workers include *Gazameda* Iredale, 1924, *Glyptozaria* Iredale, 1924, *Ctenocolpus* Iredale, 1925, *Maoricolpus* Finlay, 1926, *Spirocolpus* Finlay, 1926, *Stiracolpus* Finlay, 1926, *Zeacolpus* Finlay, 1926, *Pareora* Marwick, 1931, *Tropicolpus* Marwick, 1931, *Colposigma* Finlay and Marwick, 1937, *Leptocolpus* Finlay and Marwick, 1937 and *Sigmesalia* Finlay and Marwick, 1937.

In the following decades, workers beyond New Zealand also began to emphasize early sculptural ("apical") ontogeny in their turritellid classifications. Ida (1952) and Kotaka (1959) developed notation systems similar to and partly derived from that devised by Finlay (1930), and modified by Marwick (1957b), for describing sculptural ontogeny precisely. Merriam (1941), studying fossil species from the Pacific coast of North America, and Palmer (1937; Harris and Palmer, 1947) and Bowles (1939), studying Paleogene species from the U.S. Gulf and Atlantic Coastal Plains, also emphasized the early ontogeny of spiral sculpture. These authors did not employ a notational system such as Finlay's, using instead more ambiguous verbal descriptions based on the roots "costate" and "carinate", together with prefixes (*e.g.*, "uni-", "multi-"), to indicate the number of spirals. Although their emphasis on spiral ontogeny laid valuable groundwork for later study, the lack of precision associated with these verbal descriptions probably discouraged more detailed comparative work with taxa from elsewhere.

Allison (1965, 1967), Adegoke (1967), and Allison and Adegoke (1969) continued the tradition of Palmer, Bowles and Merriam in emphasizing early ontogeny of spiral sculpture in their work on New World fossil forms, but improved dramatically upon these earlier efforts by applying the Finlay-type notational system to apical ontogenies. This not only allowed some systematic clarification (*e.g.*, distinguishing the genus-group *Torcula* from similar forms; Allison and Adegoke, 1969) and identification and description of undescribed taxa (Allison, 1965; Adegoke, 1967), but more importantly the hypothesizing of specific evolutionary patterns of sculptural change (*e.g.*, Allison and Adegoke, 1969).

INTRODUCTION TO SYSTEMATIC PALEONTOLOGY

Species Level

Because turritellids are abundant and diverse in modern seas as well as in the fossil record, it ideally should be possible to make comparisons between paleontological and neontological species concepts in the group. To my knowledge, however, no studies have been done on intra- or interspecific variation in non-

shell characters of Recent turritellid species and, with the exception of Charles (1977), neither do detailed studies of variation in conchological characters appear to exist. Thus, as is the case with most gastropod groups (*e.g.*, Allmon, 1990), fossil species in turritellids are really no more or less equivocal than are living species. In the species descriptions given in this paper, I have analyzed patterns of shell form variation quantitatively in several taxa that seem to be especially variable and for which a sufficient number of specimens was available, and I compare these patterns to presumed population samples of a living species (the type species of the genus *Turritella*) represented in museum collections. Although such a procedure only compares ranges of shell form and not actual species status, it does represent an explicit attempt (of the only sort possible given currently available data) to link fossil and Recent species concepts. It is worth noting here that many better-studied Recent non-turritellid cerithioid species seem to show relatively high intraspecific variability in shell form (*e.g.*, Houbrick, 1974, pp.55–62), and indeed such high variation may be characteristic of most cerithioid taxa (Houbrick, pers. comm.).

Eldredge and Gould (1972, p.92) have characterized the voluminous literature on the definition and recognition of species among fossil organisms as "a theoretical debate unsurpassed in the annals of paleontology for its ponderous emptiness . . .", because in the context of phyletic gradualism it amounts to little more than a bookkeeping problem of arbitrarily parsing up continuous lineages. Eldredge and Gould got around the issue by suggesting that lineages seldom change in the phyletic mode; species tend to be more or less discrete and the problem seldom arises. This is clearly the case if ancestor and descendant overlap in time and space, resulting in a bimodal distribution of coexisting morphologies. If, however, apparent ancestor and descendant are disjunct or contiguous in time (implying a more or less wholesale transition from one to the other), then cladogenesis cannot be demonstrated conclusively, punctuated equilibrium is not applicable, and the issue of what to call various forms is important and cannot be avoided, if only for the largely utilitarian reason of recording biostratigraphically useful information. When these more problematic conditions appear to apply to the taxa discussed here, I have adopted the following working definition (modified from Beerbower, 1968, p.80–81; Waller, 1969, p.8; Gould, 1969, pp.459ff; Raup and Stanley, 1978, pp.108ff): *fossil species are groups of morphologically distinct populations within which variation is of the magnitude displayed by closely related, or presumably analogous, living species and their local populations, and between which the differences are of the kind and degree expected to result from reproductive isolation of populations in such related or analogous species.*

In a similar fashion, subspecies may usefully be recognized among fossils to designate populations separated in time and/or space and differing morphologically to a degree less than that distinguishing two species in the group (*cf.*, Newell, 1947; Gould, 1969).

SUPRASPECIFIC LEVEL

Turritellids represent a particularly conspicuous example of the problems of defining genera in fossils (Allmon, 1992a). The issues involved have been well summarized by Marwick:

> There has rarely been more reluctance to grant generic rank to subdivisions of a broad Lamarckian genus than there has been with *Turritella*. The main causes for the desire to retain *Turritella* as a world-wide, Cretaceous, possibly Jurassic to Recent genus are, no doubt, the small range in shape, the relatively simple aperture, and the general absence of well-developed axial sculpture. One rightly hesitates to grant generic significance to differences that seem trivial. When, however, such differences, on close study, emerge as reliable guides to what appear to be genetically related groups, their usefulness must not be ignored. Whether the subdivisions are accepted as genera, subgenera or sections, or neglected altogether, will depend on individual tastes, backgrounds and traditions. Much more information is needed about the animals themselves before a really satisfactory classification can be widely accepted. (1957b, p.7)

Turritellids show relatively low morphological (*i.e.*, conchological) disparity but high species diversity; what variation there is does not indicate relationship unambiguously, but rather seems to have arisen again and again throughout the history of the group (Marwick, 1957a; Kotaka, 1978; Allmon, 1987), as indicated by the general lack of concordance among the most conspicuous morphological characters. Species do not appear to form homogeneous subgroups separated by conspicuous morphological gaps.

Following the suggestions of previous authors (Merriam, 1941; Marwick, 1957a,b), Allison (1967; Allison and Adegoke, 1969) has argued that supraspecific taxa within Turritellidae should be based on differences in at least two characters, for example growth line and apical spiral ontogeny, rather than on only one. Supraspecific taxa defined by as few as two characters are still very similar morphologically, and correspond more closely to a "phylogenetic" or "cladistic" definition (in which genera can be recognized as monophyletic clades defined by as little as a single synapomorphy) than to a "phenetic" or "gap" definition (in which genera must differ by a large number of characters) (see Allmon, 1992a). In proposing supraspecific groupings for Lower Tertiary Coastal Plain turritellid species, I have followed Allison's suggestion and adopted a phylogenetic genus definition (see Allmon, 1992a for further discussion).

PHYLOGENETIC ANALYSIS

METHODS

Introduction

The central problem in a phylogenetic analysis of fossil turritellids is the small number of available shell characters. Because in a purely cladistic analysis, at least $n-1$ shared derived characters (synapomorphies) are required for n taxa, paucity of characters means that there will usually be too few characters to resolve dichotomous branching relationships fully (Eldredge and Cracraft, 1980, p.29). Rigorous cladistic analysis *can* be done on living and fossil gastropod shells (*e.g.,* Houbrick, 1985, 1987a; Erwin, 1988; Michaux, 1989; Allmon, 1990). Such analysis is possible, however, only if characters are relatively numerous (*i.e.,* at least fulfilling the above requirement) and abundant information is available on character states in other members of the group so that polarity determinations can be made (or confirmed) by either outgroup comparison or stratigraphic criteria. Neither of these conditions applies to the turritellid species considered here. Only six characters or character complexes are currently available for analysis (see below), and the states of several of these characters (especially apical ontogeny) are unknown for many other members of the group. Consequently, a purely atemporal cladistic analysis is not, for the present at least, the most productive method of phylogenetic analysis for these species.

Analysis of the species considered here has therefore proceeded at five levels: 1) species recognition, 2) grouping Coastal Plain species into morphological species groups, 3) hypothesizing and testing relationships of these species groups to each other, 4) hypothesizing and testing branching order among species within each group, and 5) hypothesizing and testing relationships among Coastal Plain species groups and other Recent and fossil turritellid supraspecific groups.

In grouping species together, and in hypothesizing relationships among species groups (steps 2 and 3 above), an explicitly cladistic approach has been taken. Species and species groups are linked together on the basis of presumed shared derived (synapomorphic) rather than shared primitive (symplesiomorphic) characters (*i.e.,* overall similarity). Given that perfect concordance among characters is not obtained, the small number of characters currently available for analysis makes it impossible to seek other characters to corroborate one hypothesis of relationship over another (*cf.,* Eldredge and Cracraft, 1980; Wiley, 1981; Cairns, 1984; Sharkey, 1989). An explicit character weighting scheme has therefore been employed.

Character Weighting

Character weighting has been criticized by some authors (*e.g.,* Eldredge and Cracraft, 1980; but see Wiley, 1981, p.141), who emphasize that all synapomorphic characters are useful in phylogeny reconstruction. As emphasized by Wheeler (1986), however, analytical errors in identifying synapomorphies at their appropriate hierarchical levels are not uncommon. Weighting expresses one's degree of confidence that a particular character is a synapomorphy at the appropriate level. Viewed in this context, the issue is how best to go about determining character weights.

Mayr (1969, pp.220ff) has suggested several criteria by which "characters with high weight" could be identified, including complexity, constancy, function and correlation. Wheeler (1986, p.107) suggests that characters "not known to occur multiple times in related taxa" are of highest value for cladistic reasoning. Neff (1986) and Wheeler (1986) both express reservations about basing such judgements on *a priori* assumptions about some inherent quality of characters themselves. Wheeler favors *a posteriori* weighting, "after characters have been critically reexamined and parsimony has failed to yield an unambiguous solution to conflicting characters" (1986, p.107). Neff suggests that a "rational basis" for *a priori* weighting is provided by asking "how much do we think we know" about a particular character. All of these criteria are reducible to expressions of confidence in synapomorphy identification. Sharkey's (1989) recommendation for weighting by compatibility (= concordance) of characters appears valid, but is of limited utility given a paucity of characters.

Following the suggestion of Wheeler (1986, p.106), character weighting in this paper consists of "simply the statement that among the evidence in conflict some characters seem less likely to be misinterpreted than others", rather than of any sort of numerical scoring. Specifically, growth line form has been given greater weight at the level of all Coastal Plain species, and apical ontogeny at the level of species groups within the Coastal Plain. These decisions are based partly on an *a priori* subjective judgement of complexity; growth line and apical ontogeny both appear to be more complex than whorl profile, size or apical angle. They are also, however, based on the relationship between these two characters and geographic distribution: all of the Coastal Plain species discussed here have a generally similar growth line trace (see discussion below), suggesting that this is a shared derived character at the level of all Coastal Plain Paleogene species.

Within the species groups resulting from this analysis, too few characters are currently available to produce fully resolved cladograms. The characters allow-

ing discrimination of species consist largely of continuously varying, poorly nested differences in size, whorl profile and adult sculpture, which are difficult to polarize. The nature and paucity of these characters results in a large number (> 100) of equal-length cladograms being generated in strict parsimony analyses using PAUP (Phylogenetic Analysis Using Parsimony), version 3.0 (Swofford, 1990). Consensus trees based on these cladograms (*e.g.,* Rohlf, 1982) include polychotomies containing most of the species. Thus to reconstruct branching order a modified stratophenetic approach has been used.

The logic and methods followed in this analysis are consistent with those used in a previous study (Allmon, 1990), and also with the arguments of Lazarus and Prothero (1984). Phylogenetic inference based solely or largely on the stratigraphic position of known fossils has a probability of being correct proportional to the quality of the stratigraphic record (Fortey and Jeffries, 1982; Allmon, 1989). When the record is relatively incomplete, an atemporal, strictly morphological analysis has a higher probability of yielding correct results than an analysis relying on stratigraphic data alone. The success of such a morphological analysis, however, will be limited if the organisms lack abundant, discrete, hierarchically nested characters not greatly prone to homoplasy. The degree to which cladistic and stratophenetic methods are used should be dependent upon the nature of the stratigraphic and morphological evidence available. The stratigraphic record here is of moderate to high completeness, and the morphology of the species is poorly suited for cladistic methods; I have therefore used a "compromise" approach combining the two methods (see further discussion in Fortey and Jeffries, 1982; Allmon, 1989).

With this in mind, the order of first appearance of species within species groups in the stratigraphic record has been taken as the primary indicator of their branching order. This still leaves, however, a substantial number of uncertain branch points. These uncertainties cannot be resolved fully at present, but qualitative "confidence limits" can be placed on many of these points by making use of the distribution of fossiliferous beds within the Coastal Plain section.

Observed stratigraphic ranges almost always underestimate true durations of taxa (Marshall, 1990). It is reasonable to assume, therefore, that observed first appearances postdate actual evolutionary originations. Strauss and Sadler (1989) and Marshall (1990) have presented methods for calculating confidence intervals for first and last appearances, but these techniques are applicable *only* if fossiliferous horizons are randomly distributed. This is not the case in the Coastal Plain Paleogene (Toulmin, 1977; Allmon, 1988b, 1989), and other methods must be sought.

Most of the fossil mollusks from the Gulf Coastal Plain come from a small number of highly fossiliferous, vertically and laterally restricted, glauconitic sands and clayey sands, distributed irregularly both stratigraphically and geographically, and separated from each other by thick, laterally extensive units of sparsely fossiliferous sands and clays. These high-density, high-diversity fossil beds represent a combination of the effects of higher density and diversity of organisms, lower sedimentation rates, and a higher proportional preservation potential of the organisms present (*cf.,* Kidwell, 1986; Cummins *et al.,* 1986). To the degree that the last factor applies, such horizons represent more reliable records of what species were present during their deposition than do less fossiliferous units. A correlated effect is that substantially more paleontological attention has been given to these highly fossiliferous units and so knowledge of their faunas is probably more complete.

The distribution of these fossil beds in the stratigraphic column can provide crude confidence levels for observed first appearances. Assuming that if a species was present, it would be more likely to be preserved and found in a very fossiliferous than a less fossiliferous interval, degree of confidence in an observed first occurrence can be expressed as the interval between observed first appearance and the youngest highly fossiliferous bed below that appearance. The closer an apparent first appearance is to a highly fossiliferous bed the smaller the uncertainty in time of actual first appearance because the fossil-rich bed is assumed to provide a maximum age. Results of such an analysis for Coastal Plain turritellid species are given in Table 2.

The high diversity, morphological simplicity, and imperfect fossil record of turritellids in the Coastal Plain may seem to amount to such a limitation of data that no firm phylogenetic and evolutionary conclusions can ever be drawn. My own response to this suggestion in the present context is admirably expressed by Wheeler (1986):

> I find reaching "no conclusion" as uninspiring as any other investigator, but we work in a less than perfect world. Rather than simply finding characters and recognizing their level of significance in the hierarchy, we are relentlessly faced with data sets so small that perturbations caused by convergent evolution mask the historical pattern we seek to discover. Such empirical constraints in the real world sometimes create situations wherein the researcher has to give up in the face of adversity or make less than idealistic methodological concessions. My position is that so long as the researcher—and the user community—recognize the inherent weaknesses in strict application of parsimony to complex data sets or the use of ad hoc weight-

Table 2.—Confidence estimates for date of first appearance of turritellid species from the Paleocene and Eocene of the Coastal Plain.

Species	*location*[1]	*observed first appearance*[2]	*next oldest high-density horizon*[3]	*maximum possible error (my)*[4]	*error as percent of total duration*[5]
alabamiensis	CG	CL	—	—	—
aldrichi	CG, EG	CL	—	—	—
alveata	CG	MB	GS	0	0
apita	CG	GS	SCB/DBT	~7	2300
arenicola	CG, EG	MB	GS	0	0
biboraensis	WG	KI	—	—	—
carinata	CG, EG?	UL	SCB/DBT	0	0
claytonensis	CG	CL	—	—	—
clevelandia	WG, CG	MB	GS	0	0
cortezi	WG	CM	SCB	0	0
creola	WG	WE	BA	~8	267
creola	CG	MB	GS	0	0
dumblei	WG	SCB	WE	0	0
dutexata	WG	WE	BA	~8	267
eurynome	CG	NF	MLM	1.3	22
femina	WG	WE	BA	~8	267
gilberti	CG	BA	TSBL	~1	31
hilli	WG	KI	—	—	—
humerosa	AT	AQ	BS	3.0	94
infans	WG	CM	SCB	0	0
kincaidensis	WG	KI	—	—	—
levicunea	CG	CL	—	—	—
lisbonensis	CG	LL	BA	~8	133
mortoni mediavia	CG	CL	—	—	—
mortoni mortoni	AT	AQ	BS	3.0	94
multilira	CG	NF	MLM	1.3	50
perdita	CG	MB	GS	0	0
pleboides	WG	CM	SCB/DBT	0	0
mortoni postmortoni	CG	NF	MLM	1.3	22
mortoni "premortoni"	AT	BS	—	—	—
praecincta praecincta	CG	NF	MLM	1.3	22
praecincta virginiensis	AT	AQ	BS	3.0	94
"prehumerosa"	AT	BS	—	—	—
rina	CG	LL	BA	~8	114
rivurbana	CG, WG	MB[6]	GS	0	0
subrina	CG	LL	BA	~8	114
tennesseensis	CG	CL	—	—	—

[1] Abbreviations: WG, western Gulf (Texas, Louisiana); CG, central Gulf (Mississippi, Alabama); EG, eastern Gulf (Georgia, western Florida); AT, Atlantic coast.

[2] Abbreviations of lithostratigraphic units same as in Table 8.

[3] Definition and origin of "high-density" fossil beds discussed in Toulmin (1977) and Allmon (1988b, 1989); stratigraphic distribution of these units shown in Text-figure 15. For taxa showing their first appearance in the Lower Paleocene Kincaid and Clayton Formations, no underlying bed is designated, since the sedimentology and taphonomy of coastal plain shell beds has not yet been investigated. It is important to note that there is as yet no positive evidence to support either continuity of discontinuity of particular turritellid lineages across the Cretaceous-Tertiary boundary in this region. For the purposes of this analysis it is assumed that all known Lower Paleocene species arose in the Lower Paleocene.

[4] Taxa are assumed to have existed throughout entire duration of any lithostratigraphic unit in which they occur. Biostratigraphic dates of boundaries of units discussed in Toulmin (1977) and Allmon (1988b). Absolute time scale that of Berggren *et al.* (1985).

[5] Total observed durations of species given in Table 8.

[6] Allison and Adegoke (1969) have reported a subspecies of *T. rivurbana* from "Undifferentiated strata of latest middle Eocene age" in Chiapas, Mexico. On the U.S. Coastal Plain the earliest occurrence is in the Moodys Branch Formation.

ing assumptions to resolve homoplasy, then perhaps these maneuvers are preferable to giving up. After all, the cladogram does represent a testable hypothesis and, if the number of available characters increases in the future, poor assumptions about weights will be shown for what they are. (1986, pp.108–109)

Geography as a Taxonomic Character

Use of geographic distribution in phylogenetic analysis is problematic because there is no necessary link between recency of common ancestry and geographic

proximity. The issue often arises in biogeographic studies, in which the goal may be to reconstruct the geographic history of a group. To use geography as a measure of relatedness and then explain the geographic pattern using the resulting phylogeny is clearly tautological. Yet if the object is not biogeographic, but phylogenetic reconstruction, the reasoning need not be circular. Geographic distribution may in certain cases be a useful taxonomic character, because related taxa often (though by no means always) occur in the same general area, a line of reasoning dating to Wallace's "law which has regulated the introduction of new species" (1855). As Mayr (1969, p.141) puts it, "there is a high probability that related species in an area are descendants of a common ancestor and that in the majority of cases no other species of this group occur disjunctly at a far distant place". (Nelson and Platnick (1981, p.384) reach exactly the opposite conclusion, stating that "Vicarious distributions are less common among distantly related taxa, such as genera within a family . . . Distantly related taxa tend to be sympatric . . .".) Mayr suggests that "Geographical characters are among the most useful tools for clarifying a confused taxonomic picture and for testing taxonomic hypotheses" (1969, p.140; see also Simpson, 1961, p.74). Essentially the same reasoning underlies Hennig's (1966, p.172) "biogeographic method", which uses geographic range changes to assist in deriving minimum ages of sister-group relationships.

In Turritellidae, Marwick (1957a) makes explicit use of geographic distribution to corroborate relationships based on morphological characters and to identify homoplasy:

> An important factor responsible for much of the confusion [in turritellid classification], has been the failure of many, but not Iredale [1924, 1925] or of Merriam [1941], to realize the strict geographic limits of most of the 'subgeneric' groups [in the family]. (1957a, p.144)

> Similarity in shape and in adult sculpture is not sufficient to transcend geographic regions. Close agreements in outer lip characters and in primary spiral ontogeny are essential for generic grouping, and even then the possibility of convergence of distant stocks with simple characters must be considered. (1957a, p.158)

Similarly, Allison (1967, p.252) suggests that the "finite and recognizable stratigraphic and geographic distribution" of many turritellid genus-groups contributes to their recognizability. (Discussing bryozoans, Boardman *et al.* (1970) have argued along the same lines for taxonomic evaluation (and generic recognition) of phenetic clusters of specimens based on their occurrence in time and space.)

Marwick (1957a,b) bases his use of geographic range on the belief that turritellids have relatively restricted dispersal ability. While noting that some species probably have wide distributions, he cites Merriam (1941) as the authority for the claim that

> "Owing to their generally short free-swimming stage and their restricted bathymetric distribution . . ., the turritellas, on the whole, must have a comparatively limited colonizing ability. Therefore, in the long course of geological time, populations must have been particularly liable to isolation through water changes in the distribution of land, the depth of the sea, and also the temperature of the water." (1957b, p.8)

> "The restricted dispersal ability of many of the Turritellidae and the long period of time represented since they first appeared in the stratigraphic record . . . should mean that many distinct genera now inhabit different parts of the world." (1957b, p.9).

Direct information on the larval biology of Recent turritellids is scanty (Allmon, 1988a; Bieler and Hadfield, 1990; Allmon *et al.*, 1992; Lieberman *et al.*, 1993). Observations are available for only four living species of the traditionally recognized subfamily Turritellinae, of which one is a long-term brooder releasing crawl-away young, two have short (7–21 day) planktonic phases, and one has either a very short or no planktonic phase. It is not known whether the larvae of any of these species feed while in the plankton. No living species is known to be teleplanic (*sensu* Scheltema, 1971), *i.e.*, to have a very long, truly planktotrophic larval phase. Since turritellids appear generally to conform to Thorson's "apex theory" (Thorson, 1946, 1950; see also Shuto, 1974b; Jablonski and Lutz, 1983), their mode of larval development can be inferred from form and size of the protoconchs of fossil as well as living species (see Allmon, 1988a), and so the potential exists to test the basis of Marwick's generalization through time. Available data on protoconch size and form of fossil and living turritellid species are summarized in Table 3.

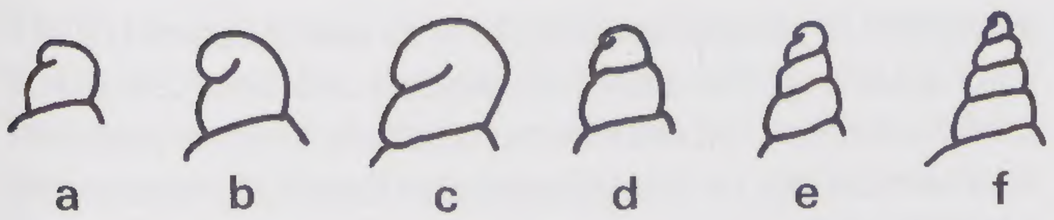
Based on these data, it would seem that turritellids have shown a variety of larval ecologies throughout their history. All Cretaceous species for which data are available (all of which occur in the Gulf Coastal Plain), as well as several species from the Neogene of the Atlantic Coastal Plain, had small, multispiral protoconchs, indicative of an extended planktonic (even if not teleplanic) phase implying high dispersal potential. Patterns are less clear for species from the Coastal Plain Paleogene. All species for which data are available have protoconchs with relatively small P1 (protoconch I), indicative of a small, yolk-poor egg and so probably planktotrophic development, but also with relatively few whorls, indicative of a relatively short stay in the plankton (Fretter and Graham, 1962, p.472; Sohl, 1977, pp.520–521; see Jablonski and Lutz, 1983 for further discussion). Observed geographic ranges of these species vary from very large to very small (Table 8, p.). A variety of protoconch sizes and forms is shown by

Table 3.—Protoconch size and inferred mode of larval development for fossil turritelline species from the U.S. Gulf and Atlantic Coastal Plains and the four living species for which these data are available. Modes of Larval Ecology: N = nonplanktotrophic, planktic or nonplanktic; SP = short term planktic, probably nonplanktotrophic; P = planktotrophic; BR = brooding. References: (1) Chapter II; (2) Lebour (1933); Fretter and Manly (1979); (3) Jablonski (1979); (4) Spiller (1977); (5) this study.

Species	age	*no. of whorls in protoconch (P1 + P2)*	*protoconch diameter (μm)*		(N)	*inferred/ observed larval ecology*	*reference*
			P1	*P1 + P2*			
variegata Linnaeus, 1758	Rec.	2.25	214	357	1	SP	(1)
gonostoma Valenciennes, 1832	Rec.	2.5	370	465	5	SP	(1)
communis Risso, 1826	Rec.		160	450		SP	(2)
gunni Reeve, 1849	Rec.	3.0	382	1080	1	BR	(1)
quadrilira Johnson, 1898	L Cret.	3.0	80			P	(3)
trilira Conrad, 1860	L Cret.	3.25	80			P	(3)
bilira Stephenson, 1941	L Cret.	3.0	80			P	(3)
howelli Harbison, 1945	L Cret.	3.5	90			P	(3)
tippana Conrad, 1858	L Cret.	3.0	75			P	(3)
vertebroides Morton, 1834	L Cret.	3.25	85			P	(3)
aequistriata Conrad, 1863	E Mio.	3–4				P	(4)
duplinensis Gardner & Aldrich, 1919	L Plio.	3–4				P	(4)
terstriata Rogers & Rogers, 1837	M Mio.-L Plio.	3–4				P	(4)
variabilis Conrad, 1830	E Mio.-L Plio.	3–5	200			P	(4)
alcida Dall, 1896	M Mio.	2–3				N?	(4)
alticostata Conrad, 1834	E-L Plio.	1.5	110			N?	(4)
burdeni Tuomey & Holmes, 1857	E Plio.	2–3				N?	(4)
chipolana Dall, 1892	E Mio.	2–3				N?	(4)
etiwanensis Tuomey & Holmes, 1857	E-L Plio.	1–2				N?	(4)
fuerta Kellum, 1926	E Mio.	2				N?	(4)
indenta Conrad, 1841	E Mio.	1–2				N?	(4)
mixta Gardner, 1947	E Plio.	2–3				N?	(4)
pilsbryi Gardner, 1928	M Mio.	1–2				N?	(4)
secta Conrad, 1855	M Mio.	1–2				N?	(4)
subannulata Heilprin, 1887	E-L Plio.	2–3				N?	(4)
subgrundifera Dall, 1892	E-L Plio.	2				N?	(4)
alabamiensis Whitfield, 1865	E-M Paleo.	2.0	94	226	2	SP	(5)
aldrichi Bowles, 1939	E-M Paleo.	1–1.5	90	199	5	SP	(5)
alveata Conrad in Wailes, 1854	L Eoc.	0.75	194	247	1	SP	(5)
apita de Gregorio, 1890	L Eoc.	2.0				N?	(5)
arenicola Conrad, 1865b	L Eoc.	2.0				N?	(5)
carinata I. Lea, 1833	M-L Eoc.	0.75	112			SP	(5)
chirena Stenzel & Turner, 1940	M Eoc.	2–2.5	112	240	1	SP	(5)
clevelandia Harris, 1896	L Eoc.	1.5	261		1	SP	(5)
creola Palmer, 1947	L Eoc.	1.0	182	250	5	SP	(5)
danvillensis Stenzel & Turner, 1940	L Eoc.	2.0				N?	(5)
dumblei Harris, 1896	M Eoc.	1.75	121	230	1	SP	(5)
dutexata Harris, 1896	M Eoc.	1.5	154	286	1	SP	(5)
femina Stenzel, 1931	M Eoc.	1.75	126	246	1	SP	(5)
gilberti Bowles, 1939	L Pal.-E Eoc.	1.75–2.0	106	238	2	SP	(5)
humerosa Conrad, 1835b	E-L Paleo.	3–4 ?				P?	(4)
mortoni Conrad, 1830	E-L Paleo.	1.75	97	280	5	SP	(5)
perdita Conrad, 1865	L Eoc.	1.75	97	223	3	SP	(5)
pleboides Vaughan, 1895	M Eoc.	1.5–1.75	109	248	2	SP	(5)
"*prehumerosa*" Govoni, 1983	E Paleo.	2.0	88	250	1	SP	(5)
"*premortoni*" Govoni, 1983	E Paleo.	2–2.5	88	291	1	SP	(5)
rina Palmer, 1937	M Eoc.	1.75–2.0	106	242	2	SP	(5)
tennesseensis Gabb, 1860	E Paleo.	2.5	85	267	1	SP	(5)

fossil and living turritellids from the Australia-New Zealand region (Text-figure 2) (Marwick, 1957b, p.8); the only fossil or Recent turritellid taxa common to Australia and New Zealand (*Maoricolpus, Colposigma,* and *Spirocolpus*), however, all have multispiral protoconchs.

If turritellid species have varied in their larval ecology and geographic range throughout their history then,



Text-figure 2.—Protoconchs of fossil and Recent turritellid species of the tribe Zeacolpini from New Zealand, showing range of form (redrawn from Marwick, 1971).

as pointed out by Sohl (1977, p.521), "It is not sufficient . . . to depend upon knowledge of the length of larval life of living species to estimate the dispersal capabilities of related fossil forms". Because protoconch size and form seem to be adequate predictors of geographic range, it is in theory possible to know in advance to what degree the species of interest were geographically restricted. Many Cretaceous and some Neogene species were widely dispersed, and Marwick's expectation of isolation and localization of related taxa would probably not apply. Most other species for which data are available (including the species under consideration in this paper), however, are consistent with the idea that turritellids did not have very high dispersal capabilities. It is therefore reasonable to assume that descendant taxa tended to inhabit regions close to those of their immediate ancestors, and that to this extent, geographic range can be used as an indicator of propinquity of descent.

Consideration of regional biogeography is also useful as an indicator of which taxa (*i.e.*, which areas) should be given more attention as potential close relatives of the taxa of interest. In the present case we may consider, for example, the biogeographic relationships of three areas with important fossil turritellid faunas that have received some degree of study: North America, western Europe, and Australia-New Zealand. Although earlier workers (*e.g.*, Finlay, 1926) have suggested that the marine invertebrate faunas of New Zealand reflected almost complete isolation since the Cretaceous, Fleming (1962, 1967, 1979) has showed that considerable faunal interchange occurred periodically throughout the Cenozoic. If these episodes could have involved turritellids then one might question the monophyly of most New Zealand turritellid supraspecific taxa. For several reasons, however, this does not appear to be the case. First, the majority of benthic marine invertebrate immigration into New Zealand during the Cenozoic was from the tropical Indo-Pacific realm. Although turritellids do occur in the latter region today and as fossils (*e.g.*, Shuto, 1974a), as a group they are not thermophilic (Allmon, 1988a), and probably never comprised an important component of the warm-water fauna of the region (although further data are required to test this hypothesis). Secondly, documented cases of immigration into the region from outside the southwestern Pacific (*e.g.*, pectinid bivalves from the Mediterranean region during the Late Tertiary, discussed by Fleming (1957) involve taxa with easily dispersed planktonic larvae.

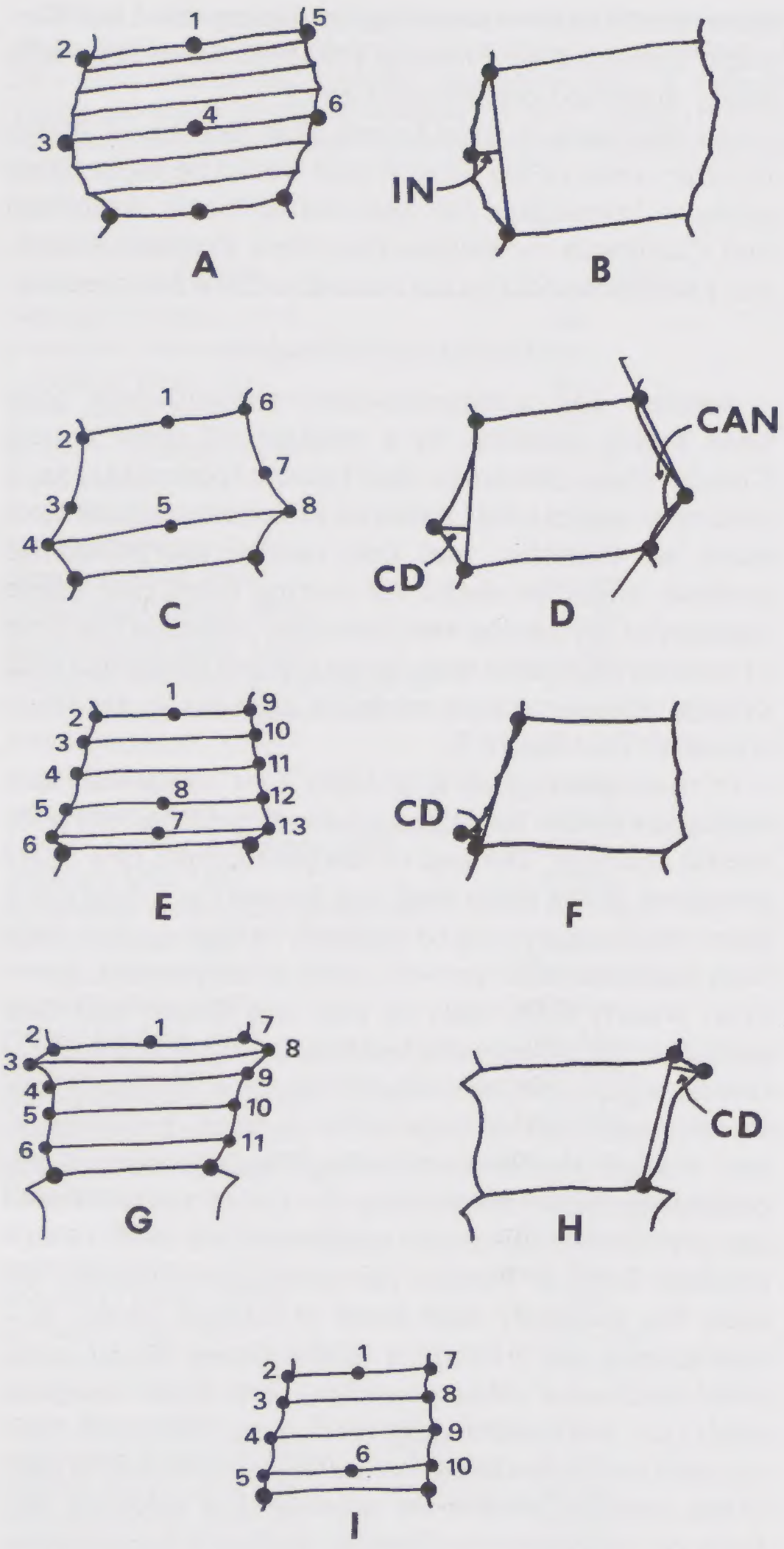
On this basis it would seem that Europe or Africa or other areas of the New World would be more likely areas to investigate for relatives of North American and Caribbean turritellids than New Zealand-Australia. These possibilities are considered in a later section.

Morphometric Analysis

Species- and subspecies-level nomenclature have been highly unstable in a number of cases among Coastal Plain Paleocene and Eocene turritellids. Such instances suggest that patterns of morphological variation are complex, and that careful morphometric analysis might be useful for sorting them out. Large samples of specimens were therefore measured for four of these problematic taxa, using a video image analysis system. Measurements made on each taxon are illustrated in Text-figure 3.

In most gastropods it is fairly easy to identify homologous points for aligning whorls prior to morphometric analysis. The end of the protoconch or a varix produced in the adult shell can be used as a landmark from which whorls can be counted. In high-spired shells with indeterminate growth, such as turritellids, however, whorls differ only in size and shape, and lack such discrete ontogenetic landmarks. Incomplete specimens, which are particularly common as fossils, are therefore difficult or impossible to align, homologize, and analyze morphometrically. This situation is undoubtedly chiefly responsible for the complete lack of any previous multivariate morphometric study of turritellids, fossil or Recent, for systematic purposes, despite the relatively high level of interest in the biostratigraphy and evolution of the group. Fossil turritellid shells are often abundant, but truly complete adult (*i.e.*, maximum size) specimens, with both protoconch and unbroken apertural lip, are extremely rare. When juvenile whorls are missing it is therefore difficult or impossible to identify similar whorl number and so to specify homologous points on shells among specimens of a given species. Construction of data matrices for morphometric analysis of a large number of turritellid specimens has thus heretofore been impossible.

For these reasons, in this study I have utilized a new computer program, "HISPIRE" (Morris and Allmon, 1994), to align specimens of single morphospecies prior to morphometric analysis. HISPIRE homologizes incomplete specimens of high-spired gastropod shells by matching whorls of similar size. It thus aligns specimens in a new data matrix, filling the remainder (missing whorls) with zeroes (= missing values for each measurement). The assumptions underlying HISPIRE are



Text-figure 3.—Measurements made on five turritellid species. Each diagram is a single whorl seen from the side. Numbered dots represent points captured as X-Y coordinates by a digitizer, from which linear measurements were calculated. Measurements are defined here as pairs of these points. Subscript p refers to point on succeeding whorl. **A.** *Turritella terebra* (Linnaeus): whorl height (WH) = 1–1_p; suture width (SW) = 2–5; whorl width (WW) = 3–6; **B.** *Turritella terebra* (Linnaeus): inflation (IN), as indicated; **C.** *Palmerella mortoni* (Conrad): whorl height (WH) = 1–1_p; carina height 1 (CH1) = 5–1_p; carina height 2 (CH2) = WH-CH1; suture width (SW) = 2–6; middle width (MW) = 3–7; carina width (CW) = 1–8; **D.** *Palmerella mortoni* (Conrad); carina depth (CD), carina angle (CAN), as indicated; **E.** *Haustator carinata* (I.Lea): whorl height (WH) = 1–1_p; carina height 1 (CH1) = 7–1; carina height 2 (CH2) = WH-CH1; suture width (SW)= 2–9; width 1 (W1) = 3–10; width 2 (W2) = 4–11; width 3 (W3) = 5–12; carina width (CW); 6–13; **F.** *Haustator carinata* (I.Lea): carina depth (CD), as indicated **G.** "*Turritella*" *praecincta* Conrad: whorl height (WH) = 1–1_p; suture width (SW) = 2–7; carina width (CW) 3–8; width 1 (W1) = 4–9; width 2 (W2) = 5–10; width 3 (W3) = 6–11; **H.** "*Turritella*" *praecincta* Conrad: carina depth (CD), as indicated; carina ratio (CR) = CW/W1; **I.** *Haustator perdita* (Conrad): whorl height (WH) = 1–1_p; suture width (SW) = 2–7; width 1 (W1) = 3–8; width 2 (W2) = 4–9; width 3 (W3) = 5–10; carina height 1 (CH1) = 6–1.

discussed in greater detail in Morris and Allmon (1994). The details of the analyses performed here are given in Appendix 1. Multivariate analysis (factor analysis) was carried out on one Recent and four fossil taxa using BMDP (1992, Program 4M).

CHARACTERS

Some indication of the utility and reliability of shell characters in phylogenetic analysis of turritellids may be obtained from the many studies that have been carried out on other cerithioid families, principally by R.S.Houbrick. In general, Houbrick (*e.g.,* 1988) contends that, at familial and higher levels, shell characters are usually unreliable indicators of phylogenetic relationships, in any case much poorer than anatomical ("soft part") characters. In the phylogenies he proposes for various cerithioid taxa at lower levels, however, shell characters often appear reasonably consistent with non-shell characters, differing chiefly in being fewer in number and so more limited in their resolving power.

For example, although he states (1984b, p.18) that "Polarities of shell characters . . . are either difficult to determine or suspect because of possible parallelisms or reversals," Houbrick bases recognition of three subgenera of *Cerithidea* Swainson, 1840 (Potamididae) principally on shell characters (*e.g.,* sculpture, form of aperture and apertural lip). Similarly, the species "*Cerithiopsis crystallina* Dall" is placed in the genus *Varicopeza* Grundel, 1982 (Cerithiidae) largely on the basis of shell characters (Houbrick, 1987b). Species of the genus *Clypeomorus* Jousseaume, 1888 (Cerithiidae), are stated to "differ from other cerithiids by their low-spired, frequently beaded shells" (Houbrick, 1985, p.1); shell characters corroborate a hypothesis of monophyly for the genus based on arrangement of the pallial oviducts and habitat requirements (pp. 7–8), and are consistent with its division into three species-groups (pp. 11–14).

Although it is possible that in the future other useful shell characters (*e.g.,* ultrastructure, developmental data on shell geometry) will become available, at present only six conchological characters or character complexes are of any real utility in phylogenetic analyses of turritellids: 1) protoconch size and form, 2) growth

line form, 3) ontogeny of spiral sculpture, 4) character of adult sculpture, 5) adult whorl profile, and 6) size. The nature of variability, apparent taxonomic value, and means of description and polarity determination for each of these characters are considered below.

Protoconch

Merriam (1941, p.9) states that the turritellid protoconch "is essentially the same in all species examined, and is similar to that of other genera—for example some of the Cerithiidae," and concludes that "The structure is too simple and generalized to be of value for purposes of taxonomy." Allison (1967) similarly has placed little taxonomic value on protoconch form, stating that "much additional study will be required before the [taxonomic] value of this structure is understood." These statements now appear to be oversimplifications. Although turritellid protoconchs share many features, they also show substantial variability which, in at least some cases, seems to have taxonomic significance.

All known turritellid protoconchs consist of between one and four or rarely five smooth, unsculptured whorls (Text-figure 2, Table 3). The protoconch I—protoconch II (P1-P2) transition (if present) is not conspicuous and the boundary with the teleoconch is marked only by the development of spiral sculpture, which may be quite faint initially. Associated with differences in whorl number and diameter are often differences in overall form, which may vary from having a first whorl well immersed within the others to an erect, high-spired cone (see Text-figure 2).

Variation in protoconch form within supraspecific groups of turritellids occurs but seems to be limited in extent. Garrard (1972, p.268) has noted that the protoconch "may vary to a small extent within a genus." Marwick (1971, p.8) has observed that in New Zealand, "Oligocene and Miocene generic groups and stocks show considerably more protoconch differences within the group than do Pliocene to Recent ones." Although Garrard states that protoconch form "remains fairly constant within species," variation within species has been reported. In the Recent Australian species *Gazameda declivis* (Adams and Reeve, 1848), the first protoconch whorl varies from depressed to erect (Garrard, 1972, p.311). One species from the Oligocene (*Tropicolpus* (*Amplicolpus*) *gittosinus* (Powell and Bartrum, 1929)) and two species from the Miocene (*Zeacolpus fyfei* Marwick, 1931 and *Z. woodhouseae* Marwick, 1971) of New Zealand each show two protoconch forms, one large, bulbous and paucispiral, the other erect and multispiral (Marwick, 1971).

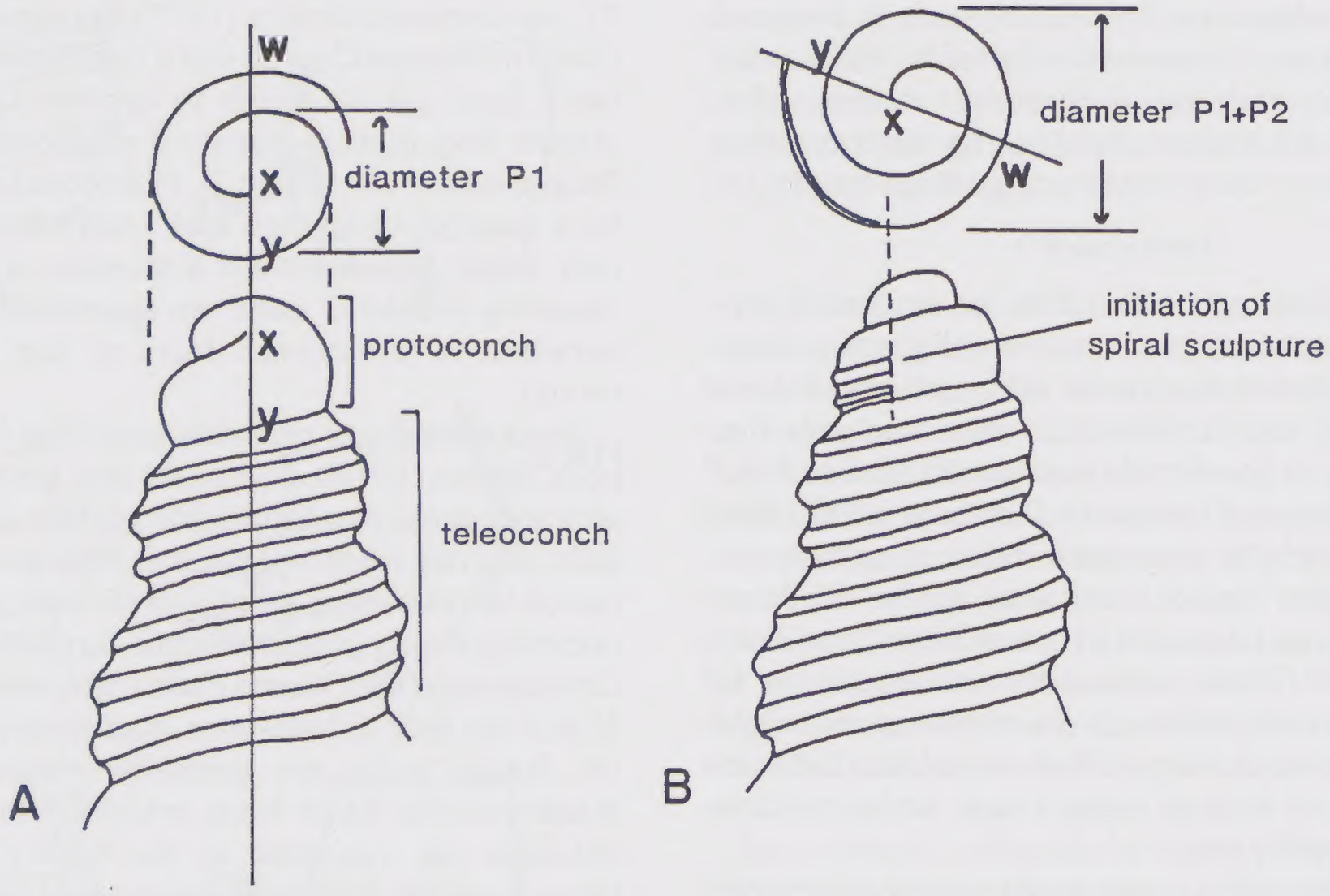
All protoconchs of Paleogene Coastal Plain species observed in the present study are similar in form (small P1, paucispiral). (Spiller [1977] has reported that *Turritella humerosa* Conrad has a multispiral protoconch, but I have not been able to confirm this.) Available sample sizes of well-preserved protoconchs of Coastal Plain species vary (Table 3). Protoconchs are unknown for a number of species, and I have been able to find only single specimens for a number of others. These sampling problems aside, no appreciable intraspecific variation in protoconch form or size has been observed.

Planktotrophy is probably primitive in mesogastropods (Shuto, 1974b; Jablonski and Lutz, 1983, p.41), although some planktotrophic species may be secondarily derived from nonplanktotrophic forms that retained larval feeding structures (Scheltema, 1978). The presence of only planktotrophic turritellids in the Late Cretaceous of the Coastal Plain (Jablonski, 1979; Table 3) and the lack of long-term planktotrophic species in the family today are generally consistent with the planktotrophic habit being primitive in Turritellidae, although the variation in the Lower Tertiary and throughout the Cenozoic suggest that the pattern may not be a simple one (see Lieberman *et al.*, 1993, for further discussion).

Ontogeny of Spiral Sculpture

Even casual examination of a turritellid shell reveals that the form of external sculpture is not constant throughout ontogeny. As noted by Palmer (1937, p.279), this variation commonly makes it difficult to identify whorls from different ontogenetic stages as belonging to the same species. Ontogenetic changes are particularly conspicuous on the earliest teleoconch whorls, when spiral sculpture is just beginning (Text-figures 4,5). The adequate description and taxonomic usage of this variation, however, have proven difficult. Finlay (1927, 1930) was the first to call attention to the importance of the ontogeny of early spiral sculpture (= apical ontogeny), and he has devised a notation system to describe it. Before discussing this system and its modifications, however, it is necessary to consider the alternative verbal system used by several American workers, two of whom studied species discussed in this paper.

Palmer (1937) uses the terms "unicarinate," "bicarinate" and "tricarinate" to describe the number of spiral ribs observed both on the earliest teleoconch whorls (= her "nepionic whorls") and on later juvenile whorls. Thus a species could be "bicarinate-tricarinate," meaning that whorls with two spirals were followed by whorls with three. Merriam (1941) and Bowles (1939) uses the terms "unicostate" for species with a single spiral rib on the earliest teleoconch whorl, "cingulate" for those with two ribs appearing roughly simulta-



Text-figure 4.—Apex of a turritellid shell, showing methods used for counting and measuring protoconch whorls. **A**. Because turritellids generally lack any conspicuous boundary marking the transition between Protoconch I (P1) and Protoconch II (P2), the diameter of P1 is somewhat arbitrarily measured along a line perpendicular to the suture at its origin (point X). Whorls in the protoconch (P1 + P2) are counted following the technique described by Marwick (1957b; taken from B. Smith, 1945): beginning at the origin of the suture line (X), one-half whorl is counted when the point Y is reached, and one full whorl at the point labeled W. **B**. The end of the protoconch (= beginning of teleoconch) is defined by the initiation of spiral sculpture (usually visible only with SEM). The protoconch illustrated consists of approximately 1.25 whorls.

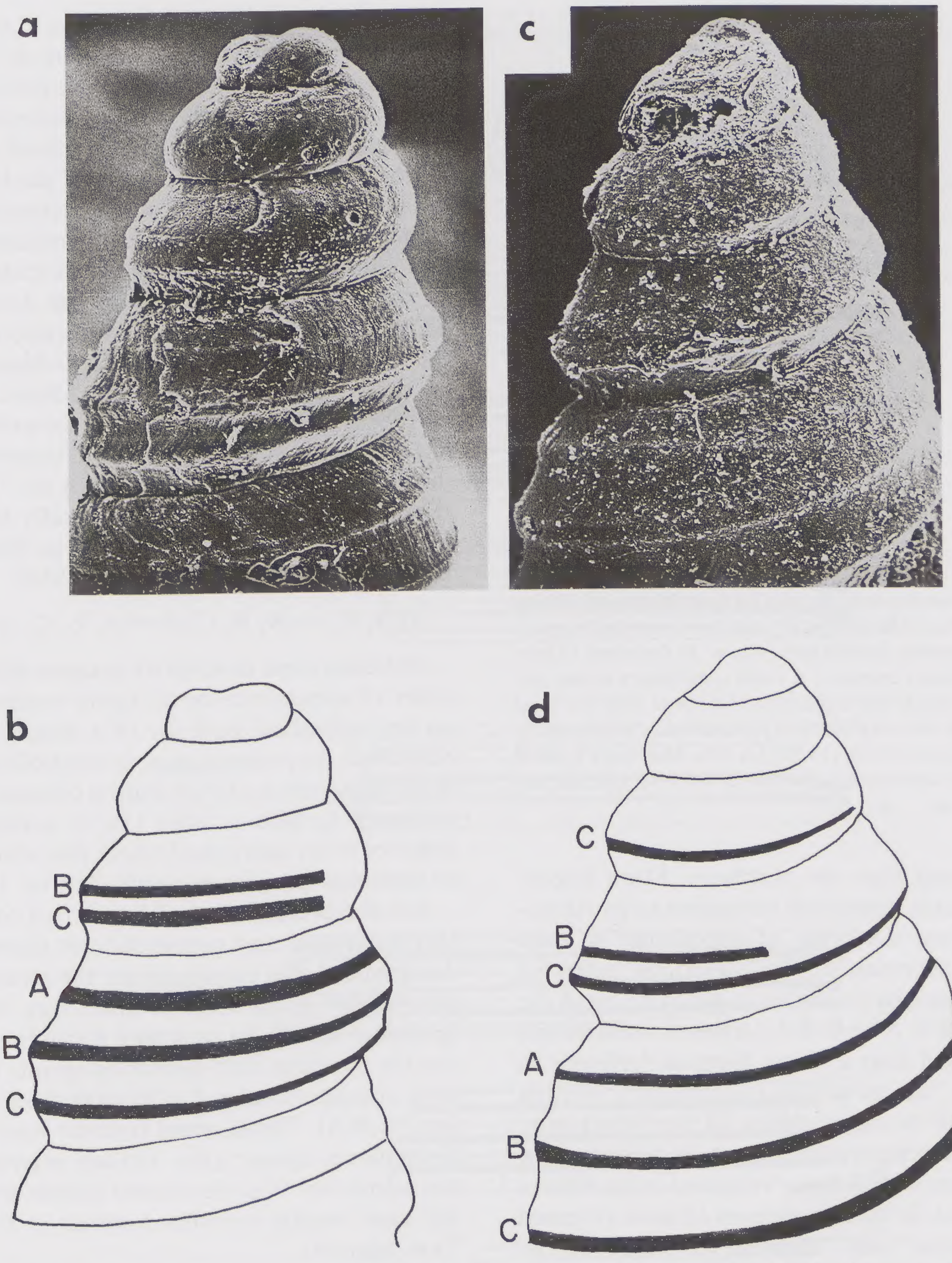
neously, "bicostate" for those with two ribs more closely spaced, "tricostate" for those with three, and "multicostate" for those with "three to six subequal revolving lirae originating almost simultaneously on the early apical whorls" (Bowles, 1939, p.270). Merriam introduces the terms "primary," "secondary" and "tertiary" to refer to the relative strengths of the spirals.

Palmer (in Harris and Palmer, 1947) has pointed out that her terms had priority, but as discussed in detail by Allison (1965, 1967), "carinate" and "costate" are used in different ways by these authors. Palmer considers only the strongest rib present in making her designations whereas Bowles and Merriam considers all ribs present. Thus a shell with three ribs appearing on the first teleoconch whorl simultaneously, but with one stronger than the other two, would be "unicarinate" in Palmer's system and "tricostate" in Merriam's and Bowles' (Allison, 1965, pp.670–671). For this reason these verbal descriptions are of little or no use in describing turritellid sculptural ontogeny (Allison, 1965), and they should be abandoned.

Finlay's (1930) system of notation is based on the observation that the vertical position of the first-appearing, or "original keels," on the whorls appears to be constant with respect to the sutures. That is, the rib appearing in the center of the whorl of one individual of a species is presumed to be homologous to the center rib in another individual of the same species and, by implication, to individuals in other species. Finlay labels the four original spirals A, B, C, and D from posterior (adapical or abapertural end, "top") to anterior (abapical or adapertural end, "bottom") of the whorl.

Ida (1952) adopts Merriam's terms primary, secondary and tertiary, but instead of using them to refer to relative strength, he used them to refer solely to order of appearance. Spiral ribs appearing first he called primary, those appearing after the primaries he called secondary, and those appearing after secondaries he called tertiary. Ida then develops a complex notation system capable of describing accurately every spiral thread on the turritellid shell. As Marwick (1957a, p.148) notes, this system is well-suited for detailed specific description, but inconvenient for brief generic differentiation.

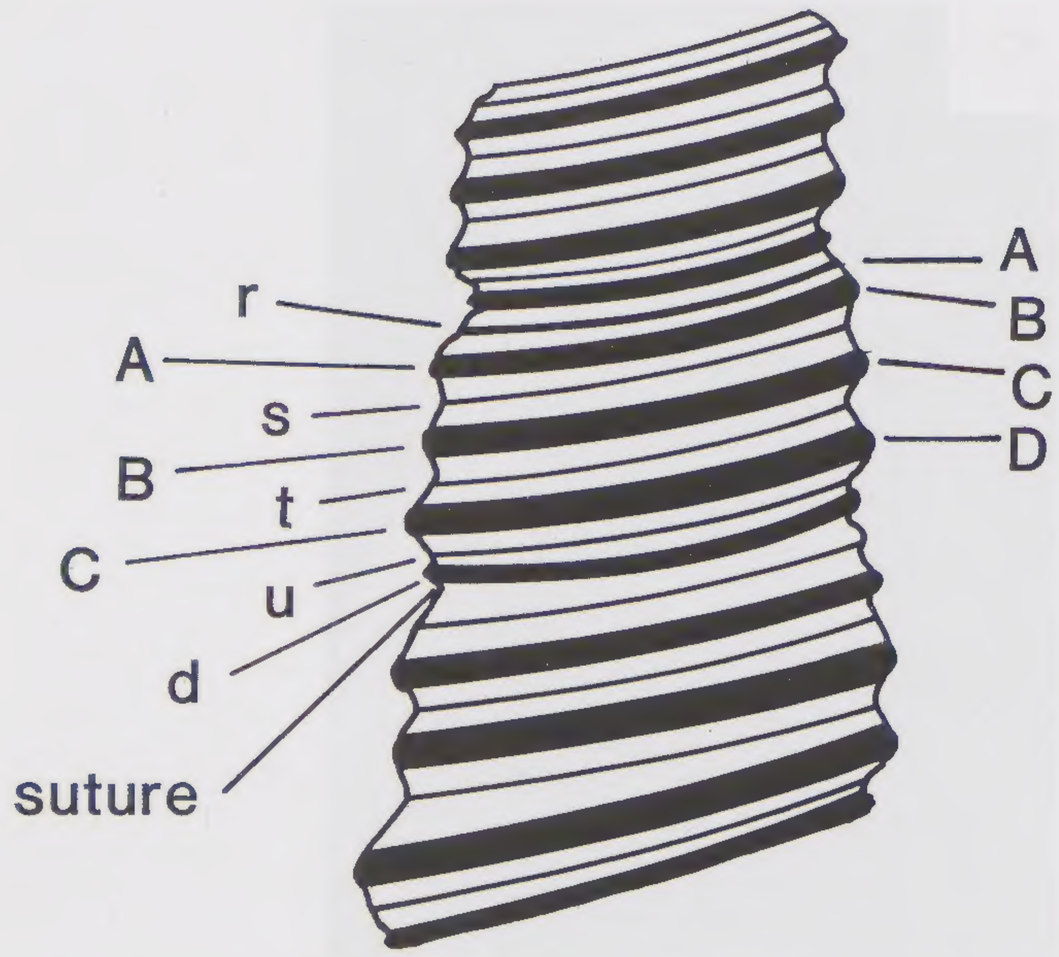
Largely independently of Ida's work, Marwick (1957b) has proposed a modification of Finlay's notation system. Instead of four primaries between upper and lower sutures, Marwick recognizes three: B at about midwhorl, A the first to appear above, C the first to appear below. The D spiral marked the base of the whorl, just above the suture. Marwick further suggests that "secondaries" (*i.e.*, in order of appearance, not



Text-figure 5.—Scanning electron micrographs of well preserved apices of two turritellid species, showing the two apical sculptural types most common among species from the Paleocene and Eocene of the U.S. Gulf and Atlantic Coastal Plains. **a**. *Turritella mortoni* Conrad from the Paleocene Aquia Formation of Virginia (160×). **b**. Sketch made from photomicrograph (a) indicating primary spiral ribs. Notation follows that described in Text-figure 6 and text. The B and C ribs appear approximately simultaneously, followed by the A rib, and so the apical sculpture formula for this species is C_1 B_1 A_2. **c**. *Turritella carinata* I.Lea from the Eocene Gosport Sand of Alabama (160×). **d**. Sketch of (c) indicating primary spiral ribs. The C rib appears first, followed by the B rib, followed by the A rib, giving an apical sculpture formula of C_1 B_2 A_3.

strength) be labeled with lower-case letters: r,s,t, and u, posterior to anterior. "Tertiaries" are "denoted by numbers according to which secondary they flank, as r1, r2, s1, s2, and so on; but generally they do not need individual designation" (Marwick, 1957b, p.13). As indicated in Figure 4, Finlay's A is equivalent to Marwick's r, B to A, C to B, and D to C; Marwick's D has no equivalent in Finlay's system.

Kotaka (1959) modifies Marwick's notation by representing primaries with lower case letters (a, b, c, d) if they were not strongly developed and secondaries by upper case letters (R, S, T, U) if they were more



Text-figure 6.—Notation systems used for describing spiral ribbing of turritellids. On the left is the system used here, essentially equivalent to that of Marwick, Kotaka and Allison, as described in text. A, B, and C are *primary* spirals, r, s, t and u *secondary* spirals. the d spiral is usually simply the angulation associated with the basal (adapertural) suture, but may be more pronounced. On the right is the system proposed by Finlay (1930); his A is Marwick's r, his B Marwick's A, his C Marwick's B, and his D Marwick's C. See text for further discussion.

strongly developed than the primaries. More importantly, Kotaka adds numerical subscripts to all rib notations to indicate the order of appearance of each individual rib. (Marwick [1957a] previously indicated order of appearance by the order in which he listed the primaries; *e.g.,* B C A or C B A.) These notations can then be combined into a single formula (referred to hereafter as an "apical sculpture formula"), written from the anterior to the posterior of the whorl (*e.g.,* $C_2\ t_3\ B_1\ s_5\ a_4$), to represent the entire spiral ontogeny. (A minor problem with Kotaka's discussion, as Allison (1967) points out, is that he appears to have reversed the terms "adapical" and "abapical" in describing the position of A, B, C and D, etc. As Allison suggests, this simple error can be disregarded and the position of the lettered ribs considered following Marwick (1957b).)

Allison (1965) modifies Kotaka's system by recommending 1) that D be included in the sculptural formula when present, but that it be given no numerical subscript due to the difficulty in determining its point of origin, and 2) that D be capitalized when it forms a prominent carina on the side of the body whorl but designated in lower case when it consists only of the angulation at the whorl base. Allison also departs from previous practice by writing apical sculpture formulas in alphabetical order from the top down. I have not adopted this last change in convention here and list the ribs from the bottom up (Text-figure 6).

Finally, Adegoke (1967) and Allison and Adegoke (1969) uses series of Kotaka-type formulas to represent not only order of introduction but sequence of changes in carina strength. For example, in the "*Turritella rina* group" the B spiral characteristically becomes obsolete, and this can be represented as follows (Allison, 1967; see Allison and Adegoke, 1969):

$$a_1\ B_1\ C_1 \rightarrow A_1\ B_1\ C_1\ d \rightarrow A_1\ b_1\ C_1\ d \rightarrow A_1\ C_1\ d$$

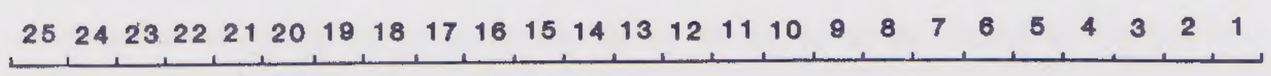
Although these descriptive systems allow the relative order of appearance of all spiral sculptural elements on an individual shell (or of a single species) to be described, they cannot present symbolically the timing of all changes in sculpture during ontogeny. The closest approach to such is Ida's (1952) system, which can describe every individual whorl, but which is also rather unwieldy (see, for example, Titova, 1994a).

For the present work, I have tried to extract from this notational and nomenclatural history a series of designations that communicate the greatest amount of information in the least complex way. For individual species, I use apical sculpture formulas listing as primaries the three first-appearing spirals from the bottom, or adapertural end, of the whorl below the C spiral (*e.g.,* C,B,A). The D spiral is at the base of the whorl. Secondaries appear after and are intercalated among the primaries. Well-developed spirals are given in upper case, weakly developed spirals in lower case (see Text-figure 6).

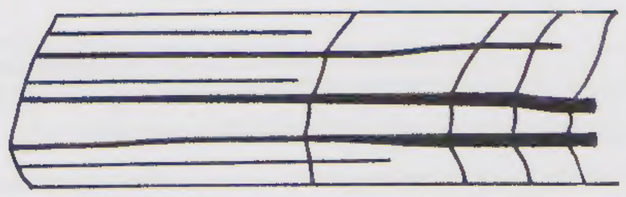
Rather than listing sculptural formulas for individual whorls, I summarize the sculptural ontogenies of turritellid species graphically. I have modified the type of diagram used first in a very simple form by Kotaka

→

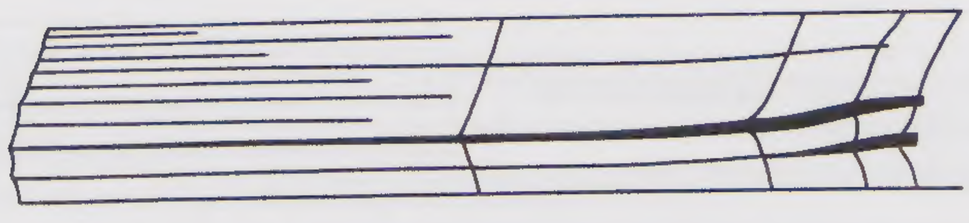
Text-figure 7.—Schematic diagrams illustrating ontogenetic development of spiral sculpture in turritellid species from the Paleocene and Eocene of the Coastal Plains. These are herein called "Marwick Diagrams" in recognition of the use of a similar technique for illustrating turritellid ontogeny by Marwick (1971). Numbers across the top represent whorl number, the protoconch and youngest whorls being on the right. Succeeding whorls are standardized to the same height. Horizontal lines represent the spiral ribs as they appear and change in strength throughout ontogeny. Curved vertical lines at intervals represent whorl profiles. Diagrams do not represent single individuals, but were constructed by counting whorl number from protoconch-teleoconch boundaries, recognized in scanning electron micrographs, then constructing "composite individuals" by assuming that whorls of similar size were the same number, and examining incomplete specimens of increasing size.



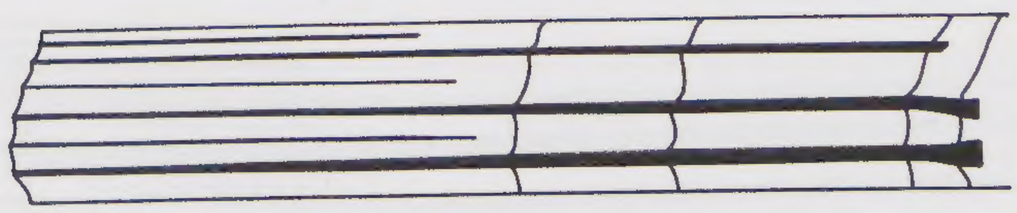
chirena



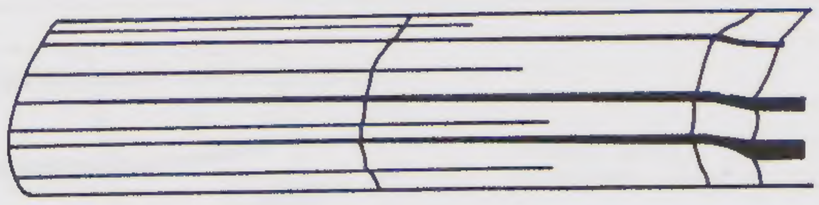
arenicola



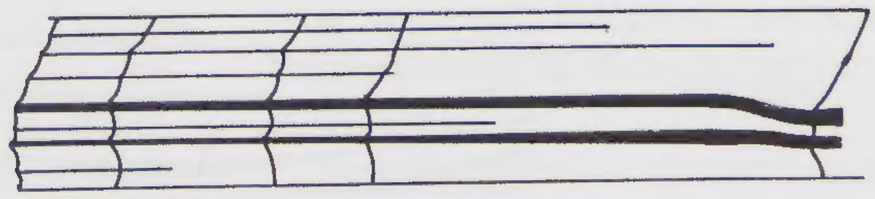
alveata



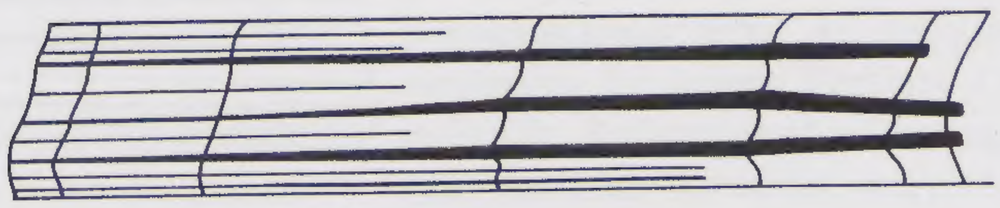
pleboides



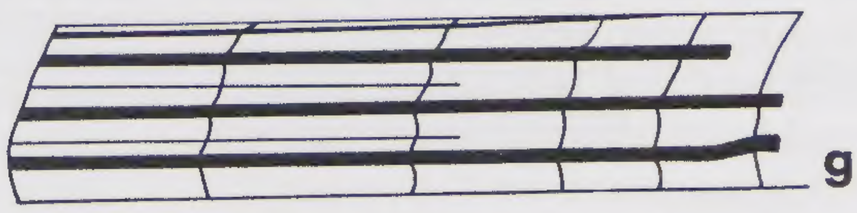
creola



dumblei

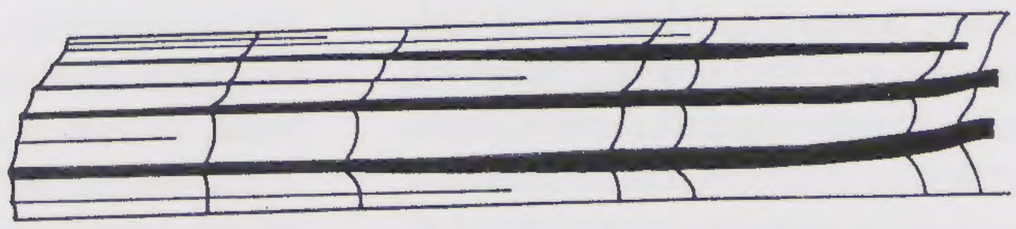


clevelandia

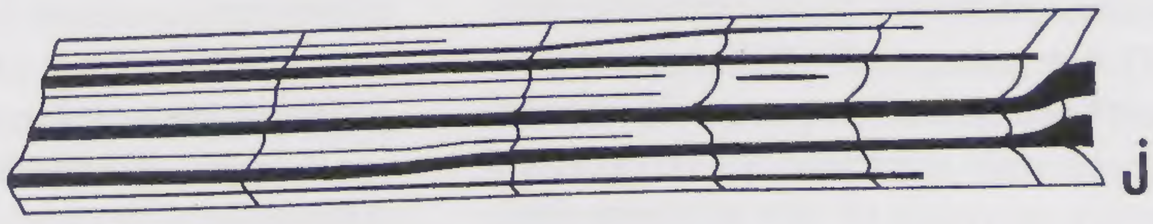


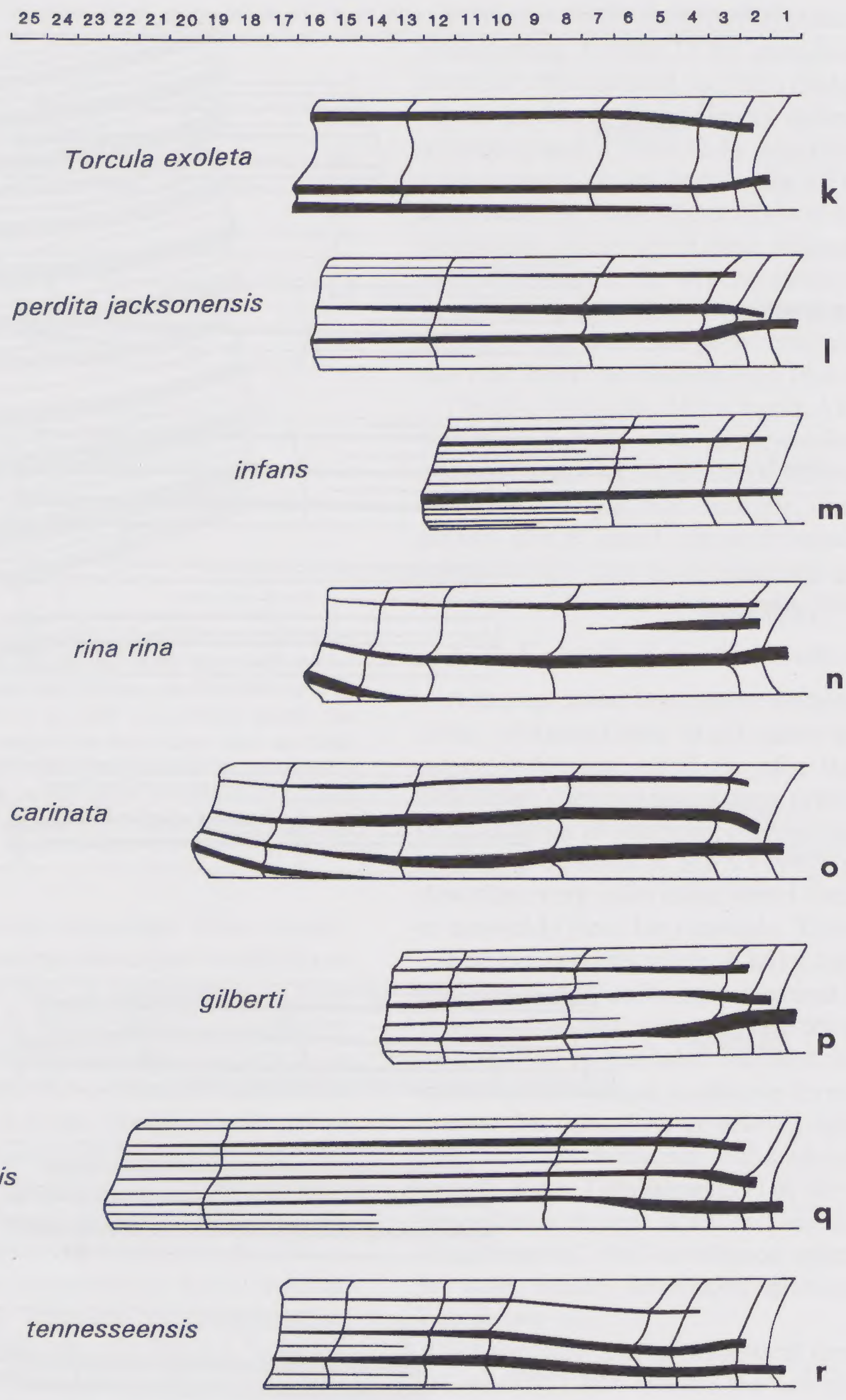
dutexata

femina



mortoni mortoni

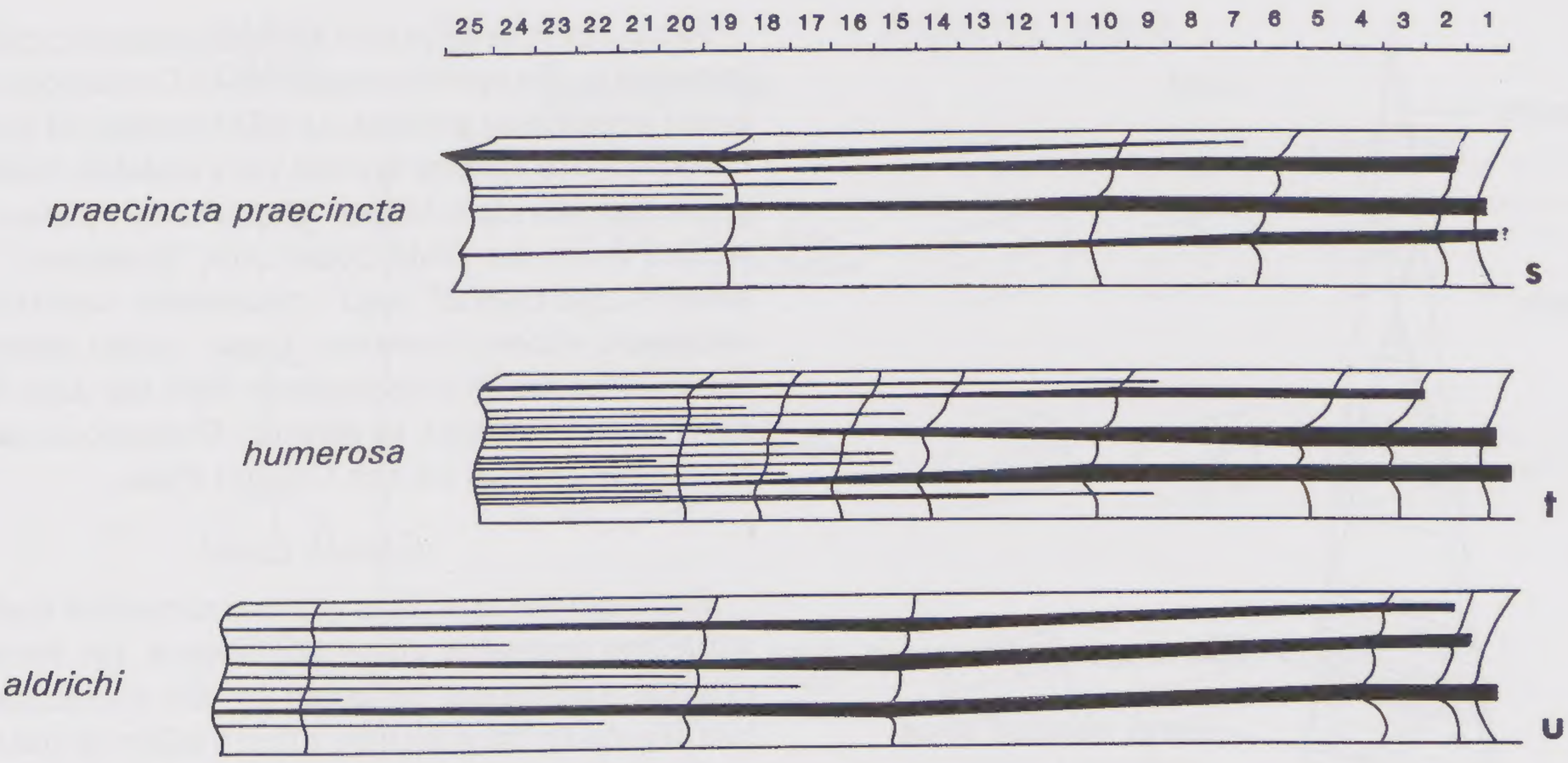




Text-figure 7.—Continued.

(1959, p.48) and developed further by Marwick (1971, p.63) for this purpose (herein referred to as a "Marwick diagram") (Text-figure 7). At supraspecific levels, however, such graphical methods are not practical (because interspecific differences within species groups are too great), and the recommendations of Allison and Adegoke (Allison, 1967; Adegoke, 1967; Allison and Adegoke, 1969) are more appropriate: supraspecific apical sculpture formulae need only summarize the order of appearance and relative strength of the primary (*i.e.*, first-appearing) spirals. For example, the generic formula for *Haustator* Montfort, 1810 is C_1 B_2 a_3 (Marwick, 1957a, p.154).

The phylogenetic importance granted here to early apical spiral sculpture is based chiefly on its relative complexity, which I believe increases chances of correct identification of homology, but also on corroboration by geographic and stratigraphic criteria. The work of Palmer, Merriam, Bowles, Marwick, Kotaka and Allison has demonstrated that coherent lineages can



Text-figure 7.—Continued.

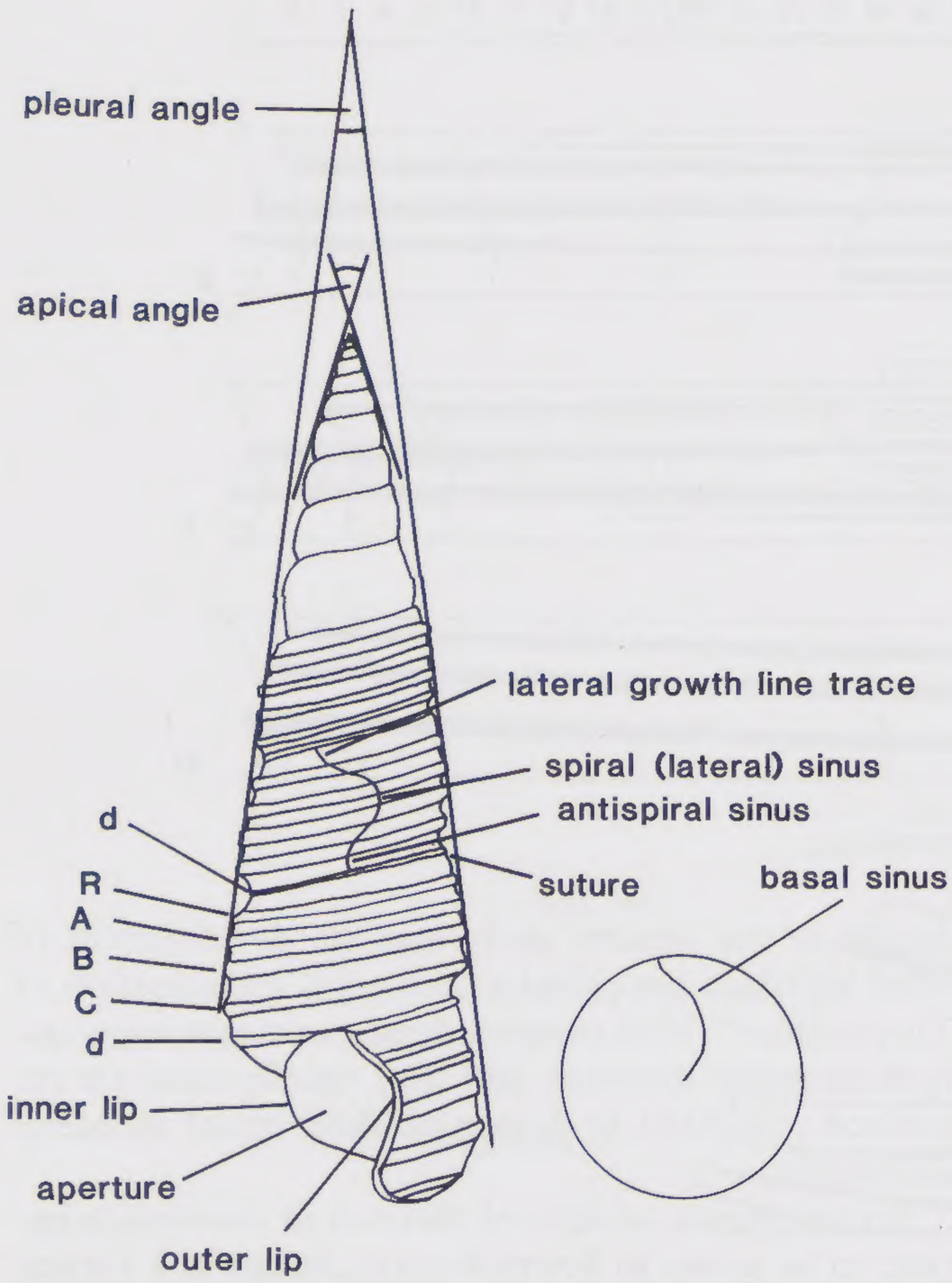
be traced mainly on the basis of apical ontogeny within a given geographic and stratigraphic context. The results presented below, furthermore, suggest substantial concordance, at least within the Coastal Plain Paleocene and Eocene, among apical ontogeny, growth line form and whorl profile. (As already mentioned, MacNeil (in MacNeil and Dockery, 1984) maintains that convergence is equally likely in early spiral ontogeny as in any other character, and implies that sculpture and whorl profile of later whorls may be of more importance. Yet he presents no specific evidence for this conclusion.)

It is important to note that all previous systematic study of turritellid apices has been done solely by means of light microscopy. Although careful examination of a large number of well preserved apices of some species by this method can reveal their earliest apical ontogeny, extensive examination of Coastal Plain species with scanning electron microscopy (SEM) in the present study has shown that this is not consistently the case. Spiral ribs may be quite faint at their inception and difficult to discern, even with SEM. As a result, species that appear to have an apical spiral formula of, for example, C_1 B_2 A_3 under the light microscope may be seen to have C_1 B_1 A_2 under SEM (*e.g.*," *Turritella mortoni* Conrad"; see Text-figure 5).

As noted by Merriam (1941, p.35), published figures and descriptions, particularly prior to the last 30 years, are usually inadequate for determination of apical ontogeny of a species with this precision. Furthermore, apical ontogenies reported by more recent workers (*e.g.*, Marwick, 1957a,b, 1971; Allison, 1965; Allison and Adegoke, 1969) based on examination with the light microscope also may prove to be incorrect. This is one of the principal factors limiting both the systematic results of the present study and the development of what Merriam has called a "universal classification of Turritellidae". Well preserved apices are rare, especially in museum material, and they usually must be examined with SEM to determine their apical ontogeny accurately.

Because spiral sculptural patterns in turritellids appear to be prone to heterochronic change in a variety of modes (Allmon, 1994), polarity of apical ontogenies is best determined by outgroup comparison, rather than ontogenetic criteria. As discussed below, choice of an outgroup for lower Tertiary Coastal Plain species is difficult. Reference to all recognized turritellid suprageneric taxa, however, may make choosing a specific outgroup unnecessary, at least for this character. Examination of apical ontogenies of other turritellids in Table 1 shows that only two groups outside the U.S. Coastal Plain (*Tropicolpus* Marwick, 1931 from the Oligocene of New Zealand and *Hataiella* Kotaka, 1959 from the Miocene of Japan) have an apical sculpture formula of C_1 B_1 A_2. Thus, unless one of these two is the sister taxon to Coastal Plain species, which seems unlikely on geographical grounds, this apical formula cannot be primitive.

Only two other apical formulae are known to be represented on the Coastal Plain: C_2 B_1 A_3 by *Turritella turneri* Plummer, 1933 and *T. dobyensis* Dockery, 1980, and C_1 B_2 A_3 by all other species. Assuming the latter to be primitive in this case is not based so much on the "commonality principle," which is of dubious validity (Watrous and Wheeler, 1981), but on stratigraphic criteria; C_2 B_1 A_3 species are known only from the Middle Eocene on the Coastal Plain, whereas C_1 B_2 A_3 species are known from throughout the Paleocene and Eocene.



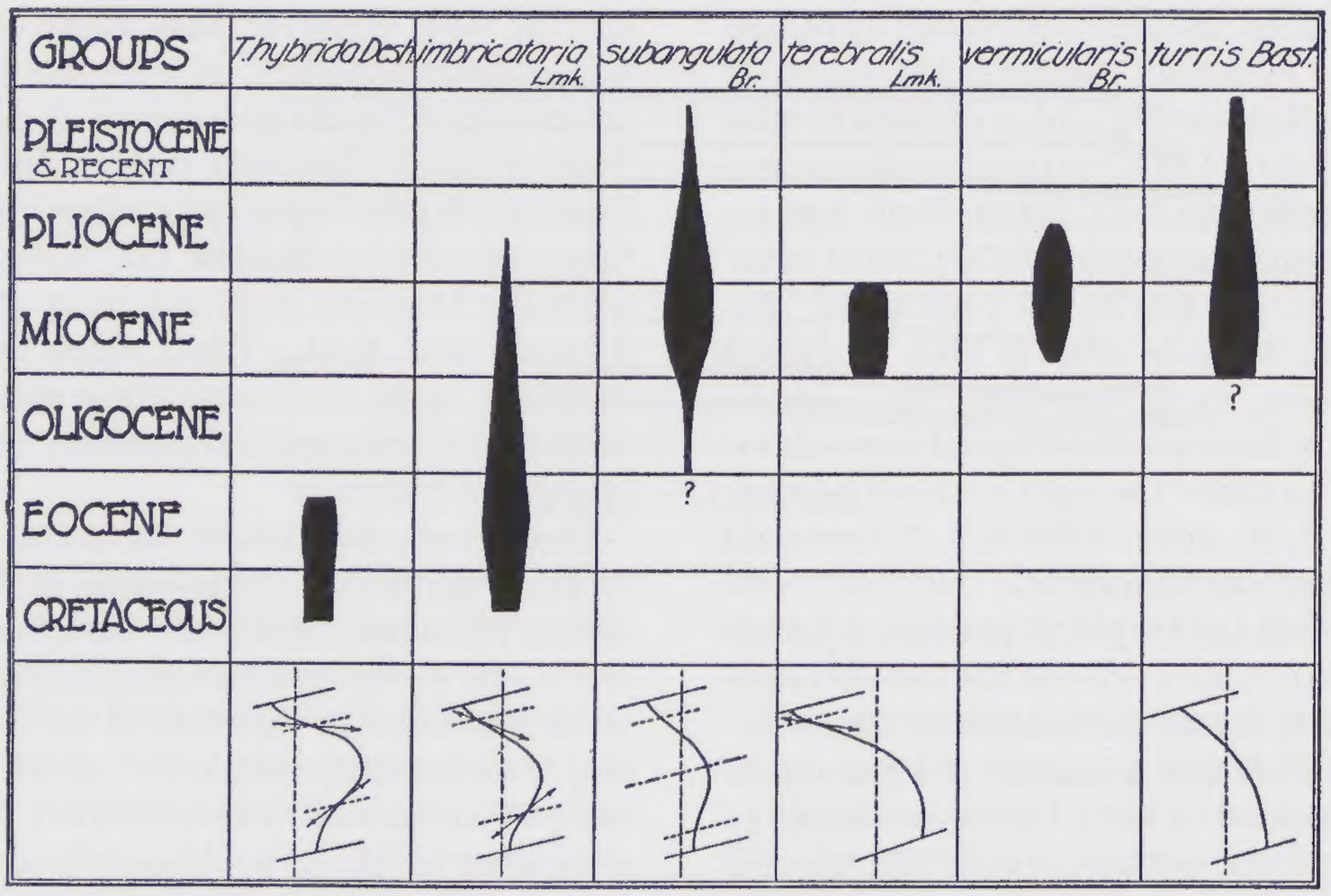
Text-figure 8.—Morphological features of adult turritellid shells used in classification and species descriptions. Circle to the right represents the base of the last whorl, looking toward the apex of the shell parallel to the axis of coiling.

More direct application of stratophenetic criteria, by recourse to the apical ontogenies of Cretaceous species, is not possible at present, as SEM studies of most Gulf Coastal Plain species are not yet available. Sohl (1960, p.71) has divided Upper Cretaceous species he describes from the Gulf Coast into "bicostate," "tricostate," "multilirate" and "placement uncertain." As discussed above, however, these verbal descriptions are of little use in comparisons with the data required here. It still remains to connect Cretaceous species to Paleogene species on the Coastal Plain.

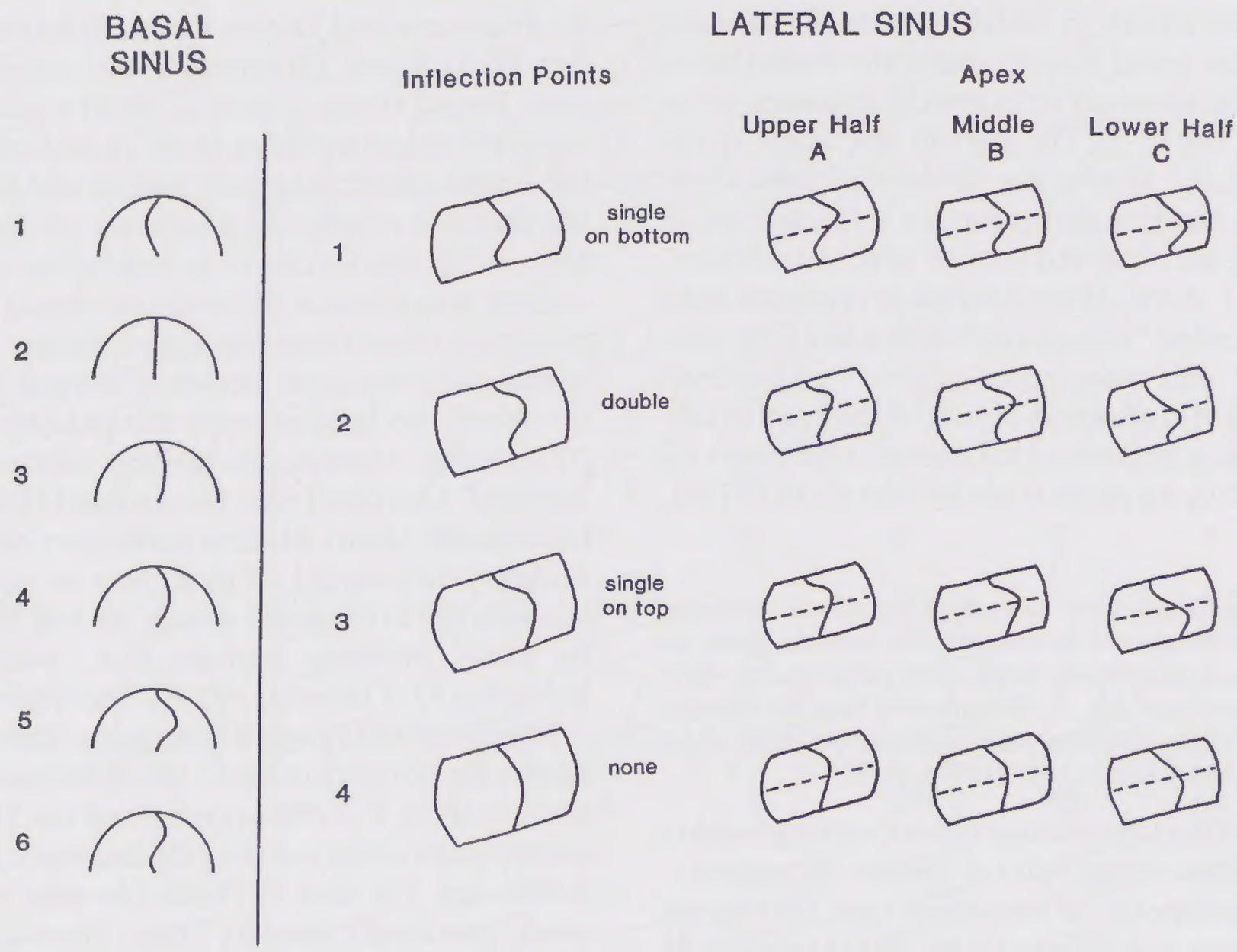
Growth Lines

Although the apertures of most turritellid shells, even while the animal is alive, are broken, the form of the original aperture is reflected by the incremental collabral growth lines that are often visible on the external surface of the shell. The growth line has two aspects, which can be termed lateral and basal (Text-figure 8). The lateral is visible on the side of any whorl, because the growth lines run between the bounding sutures. The basal is only visible on the bottom of the last whorl of the shell, where the growth lines run from the whorl periphery to the columella at the center. Guillaume's (1924) landmark paper on turritellid classification, in which he emphasizes the importance of examining growth lines, discusses only the lateral aspect (Text-figure 9), a point for which he is criticized by Dollfus (1926).

The turritellid growth line is a sinuous line bent into a third dimension. As such it has several aspects and



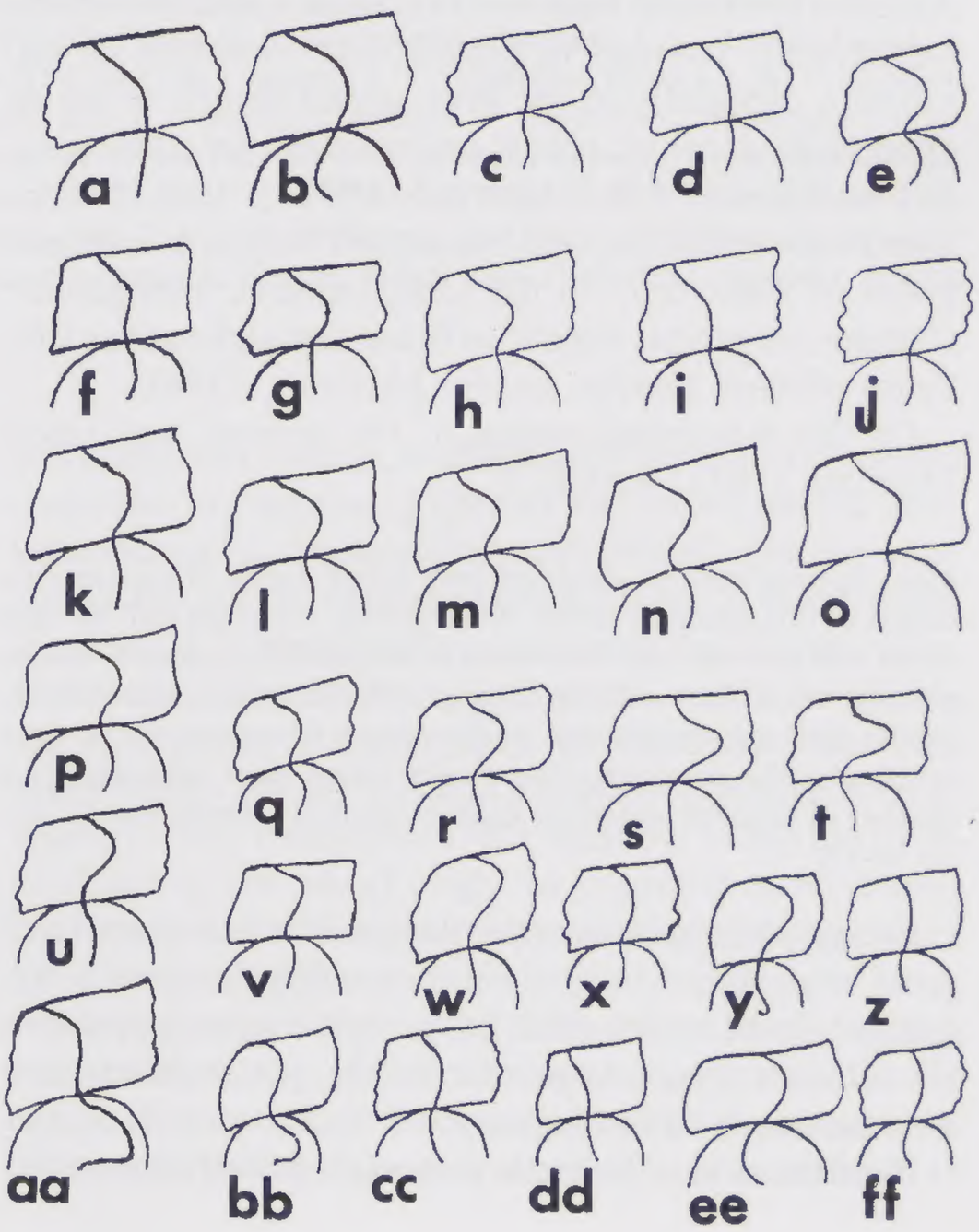
Text-figure 9.—Guillaume's classification of turritellid growth line types, and their stratigraphic distribution in the Cretaceous and Cenozoic of Europe and North America. Only the lateral aspect of the growth line was considered by Guillaume, shown here schematically with inflection points beneath its stratigraphic distribution. (From Merriam, 1941, modified from Guillaume, 1924.)



Text-figure 10.—Classification of growth line traces used in this paper (see Tables 1,9).

can be described in several ways. The most important of these are as follows (see Text-figures 9–11):

1) Lateral and basal sinuses (*cf.*, Marwick, 1957a). These are curves in the growth line visible on the lateral and basal aspects of the shell, respectively. The lateral is always concave in the "spiral" direction (Merriam, 1941); that is, toward the aperture, if only so slighly that it appears virtually straight. The basal sinus may be absent, and the growth line straight across the whorl base, but if present it is concave in the spiral or, more rarely, the "antispiral" direction (away from the aperture). 2) A third sinus, concave in the antispiral direction, may be present on the angulation at the an-



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Text-figure 11.—Variation in basal and lateral aspects of growth line trace within the family Turritellidae. (Modified from Marwick, 1957a.) All except d,u, and aa based on type species. **a**. *Turritella*, **b**. *Zaria*, **c**. *Archimediella*, **d**. *Torculoidella bicarinata*, **e**. *Kurosioia*, **f**. *Leptocolpus*, **g**. *Ctenocolpus*, **h**. *Gazameda*, **i**. *Torculoidella*, **j**. *Stiracolpus*, **k**. *Peyrotia*, **l**. *Maoricolpus*, **m**. *Zeacolpus*, **n**. *Haustator*, **o**. *Tropicolpus*, **p**. *Torcula*, **q**. *Bactrospira*, **r**. *Platycolpus*, **s**. *Colpospira*, **t**. *Spirocolpus*, **u**. *Neohaustator*, **v**. *Turritella hybrida* [referred to *Torquesia* by Marwick], **w**. *Colposigma*, **x**. *Colpospirella*, **y**. *Pareora*, **z**. *Tachyrhynchus*, **aa**. *Protoma*, **bb**. *Protoma* (*Protomella*) *knysnaensis*, **cc**. *Mesalia*, **dd**. *Neodiastoma*, **ee**. *Sigmesalia*, **ff**. *Glyptozaria*.

terior end of the whorl, in which case the basal sinus is concave in the spiral direction and the lateral sinus is relatively deep; this may be called the antispiral sinus (*cf.*, Merriam, 1941). 3) The growth line angle is the angle "between the axial plane of the shell and a line connecting the anterior and posterior terminations of the growth line as observed on the exposed surface" (Merriam, 1941, p.59). When this angle is greater than zero, it can be called "prosocline", when less than zero "opisthocline", and when equal to zero "orthocline" (*cf.*, Cox, 1960). 4) Inflection points of the growth line are emphasized as important taxonomic characters by Guillaume (1924). As pointed out by Marwick (1957a), however,

> Guillaume's 'points of inflection' suffer from the family weakness, variability, and the distance of the abapical one from the suture is, in many shells, due as much to the height of the suture on the whorl as to the shape of the outer lip. . . . Nevertheless, since the strength and distance apart of the inflection points influence the shape of the sinus, they can be highly significant." (1957a, p.147)

5) The apex of the lateral sinus falls at varying heights above the anterior suture: above, below, or approximately at the midpoint of the whorl (see Text-figure 10). 6) Growth lines and spiral ribs. In his critique of Guillaume, Dollfus (1926) states that Guillaume ignores the effects of spiral ribs on the form of the lateral aspect of the growth lines. Guillaume (1926) responds that these effects were negligible, an opinion with which Allison (1967) and I agree. 7) Ontogeny and gerontism. Ontogenetic changes in growth line form can be significant, especially in the very largest whorls in which apparently gerontic effects are manifest (*cf.*, Marwick, 1957a; Allison, 1967; Garrard, 1972, p.268). Gerontism is conspicuous, and important from a taxonomic point of view, only in the larger species; ontogenetic changes, however, appear to occur throughout the lifetimes of even smaller species (Allmon, 1994).

Of the taxonomic value of the growth line trace, Merriam (1941) writes:

> Many species may be identified with a fair degree of certainty by means of this character alone. Nevertheless, it cannot well be used as the sole basis for the foundation of subgenera or major divisions of lesser value. The curvature of the growth line is, after all, relatively simple, and not comparable to the sutures of ammonites or even nautiloids. The possibility that similar traces have originated in a number of distantly related or distinct phyla is a strong one. (1941, pp.34–35)

Despite his opinion that the growth line trace is of great importance in turritellid classification (see Text-figure 11), Marwick (1957a, p.154) also suggests that the simplest types (*e.g.*, that of the genus *Haustator*) may be prone to homoplasy.

Examination of juvenile and adult growth line traces for Paleocene and Eocene Coastal Plain turritellid species (Text-figure 12) shows some interspecific variation, but all traces appear to be of a basically similar type: the majority show three points of inflection on the lateral aspect (adapical, medial and basal, although the presence of adapical and basal points is often variable within species), have an orthocline or slightly prosocline lateral sinus of moderate depth, a shallow to moderate spiral basal sinus, and display a spectrum of apical positions from above to around the middle of the whorl; no species (with the possible exception of "*Turritella*" (herein *Palmerella*) *mortoni* ssp. ("*pre-mortoni*" Govoni, 1983; Govoni and Hansen, in press) consistently shows a lateral sinus apex below the whorl middle. They would all thus seem to agree with Guillaume's (1924) *hybrida* group, as has been suggested by many previous authors (*e.g.*, Woodring, 1928; Palmer, 1937; Bowles, 1939) (Text-figures 9,12).

Marwick (1957a, p.147) suggests that "Guillaume's figures do not do justice to the difference between the sinuses of the *T. hybrida* group and the *T. imbricataria* group," and observes that Guillaume's figures (1924, p.286, figs. 7,8, and 9) "have the apex of the *hybrida* sinus too nearly medial. They should be distinctly adapical as plainly shown by the photographs of his plate 10" (Marwick, 1957a, p.47) (see Text-figure 9). Even while emphasizing the differences between the *hybrida* and *imbricataria* lateral sinuses, however, Marwick (1957a) also seems to deemphasize them when he places in the genus *Torquesia,* erected by Douvillé (1929) for species in the genus *Haustator* Montfort, 1810 (= Guillaume's *T. imbricataria* group), many Cretaceous species of Guillaume's *hybrida* group (1957a, p.160). Indeed Guillaume himself (1924, 1926) states that the differences between his *hybrida* and *imbricataria* groups are not profound. Although Guillaume's (1924) plates do show the subtle difference in height of the apex of the lateral sinus mentioned by Marwick, my own examination of specimens of these species (*Turritella hybrida* and *T. imbricataria*) suggest that this difference is variable (Text-figure 12-ll,mm).

In summary, it is not clear that the *hybrida* and *imbricataria* lateral growth line groups of Guillaume are distinct. All lower Tertiary Coastal Plain species show a similar lateral growth line aspect which they may share with many Eurasian species from both the Cretaceous (genus *Torquesia* Douvillé, 1929) and lower Tertiary (genus *Haustator* Montfort, 1810, and one or more probably unnamed groups; see discussion below). The growth line form of these Coastal Plain species would therefore appear to be a shared primitive character, not useful in sorting out their relationships with each other or with their closest relatives in Eurasia.

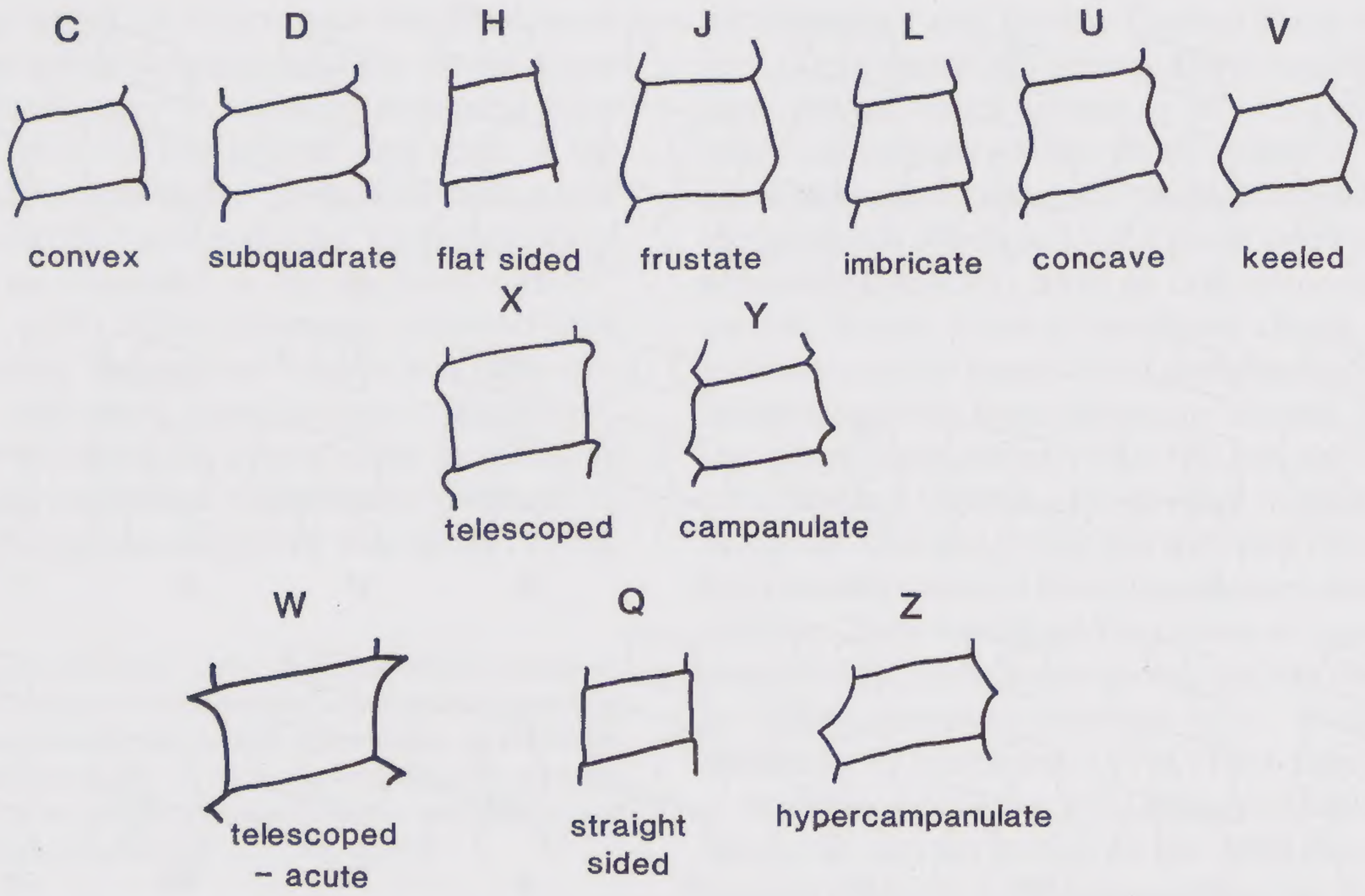
Text-figure 12.—Growth line traces of turritelline species from the Paleocene and Eocene of the Gulf and Atlantic Coastal Plains. **a**. *T. mortoni* Conrad, **b**. *T. hilli* Gardner, **c**. *T. "premortoni"* Govoni, **d**. *T. levicunea* Harris, **e**. *T. kincaidensis* Plummer, **f**. *T. dumblei* Harris, **g**. *T. femina* Stenzel, **h**. *T. dutexata* Harris, **i**. *T. chirena* Stenzel and Turner, **j**. *T. apita* de Gregorio, **k**. *T. lisbonensis* Bowles, **l, m**. *T. pleboides* (Vaughan), **n**. *T. creola* Palmer, **o**. *T. alveata* Conrad, **p**. *T. clevelandia* Harris, **q, r**. *T. arenicola* (Conrad), **s**. *T. danvillensis* Stenzel and Turner, **t**. *T. tennesseensis* Gabb, **u**. *T. alabamiensis* Whitfield, **v**. *T. gilberti* Bowles, **w**. *T. rina* Palmer, **x**. *T. subrina* Palmer, **y**. *T. carinata* I.Lea, **z, aa, bb**. *T. perdita* Conrad, **cc**. *T. infans* Stenzel and Turner, **dd**. *T. rivurbana* Cooke, **ee**. *T. "prehumerosa"* Govoni, **ff**. *T. aldrichi* Bowles, **gg, hh**. *T. humerosa* Conrad, **ii**. *T. multilira* Whitfield, **jj**. *T. eurynome* Aldrich, **kk**. *T. praecincta* Conrad. Non-coastal plain species presented for comparison: **ll**. *T. hybrida* Deshayes, Eocene, Europe, **mm**. *T. imbricataria* Lamarck, Eocene, Europe, **nn**. *T. terebra* (Linnaeus), Recent, Pacific, **oo**. *T. robusta* Gryzbowski, Miocene, South America.

Whorl Profile

Whorl profile here refers to the overall shape of the whorl independent of the effects of the spiral ribs. Although in practice this can sometimes be a difficult distinction to make by eye, it is readily accomplished via x-radiographs, camera lucida or analytically from morphometric data. Ida (1952) has proposed a set of whorl profile types designated with letters. Marwick (1971) adds names to the types. I have added two more types for the system employed here (Text-figure 13). These "types" are not intended to be interpreted as discrete character states, but only as end members of a multidimensional morphological continuum useful for identification and description.

Although it is one of the most conspicuous aspects of a turritellid species, and was long the most important character in diagnosing species and supraspecific taxa, whorl shape is of uncertain status in phylogenetic analyses of the group because of the problem of homoplasy. *A priori,* it is reasonable to suppose that of the characters considered here, whorl profile might be among the most prone to homoplasy. To the degree that shell morphology is functional in gastropods generally (*e.g.,* Signor, 1982; Hickman, 1985; Stanley, 1988) the overall shape of the whorl might be expected to be among the first shell characters to respond to selection pressure (*cf.,* Ponder, 1973).

Also of importance is the difficulty of homologizing whorl shape, the step that must precede the identification of homoplasy. Without more developmental information that is currently available, it is difficult or



Text-figure 13.—Classification of adult whorl profiles in turritelline gastropods. Lettered types C-Y first distinguished by Ida (1952), to which descriptive terms were added by Marwick (1971). Types Q, W and Z are distinguished here for the first time, as variations on types X and Y.

impossible to say whether a similar whorl profile in one turritellid species is the "same" as that in another. One technique that has been successful in this regard has been use of presumably homologous primary spiral ribs on the late whorls. For example, the two species *Turritella* (herein *Palmerella*) *mortoni* Conrad and *T.* (herein *Haustator*) *rina* Palmer are both basally carinate in whorl profile. Yet in *mortoni* the carina is composed of the C spiral, whereas in *rina* it is composed of the D spiral (Allmon, 1987, 1994).

Without more knowledge of the direct Cretaceous ancestors of the lower Tertiary Coastal Plain species, or of their closest relatives in Eurasia or elsewhere, it is difficult to specify the polarity of whorl profile change in these species. The possibilities can be generalized to three, which are evaluated in the phylogenetic analyses below; the ancestor of the Coastal Plain species could have had 1) a round, 2) an adapically carinate, or 3) a basally carinate adult whorl profile. Few data are currently available to support one or another of these alternatives. The generally non-carinate whorl shape of most Cretaceous species from the Gulf Coastal Plain (*e.g.*, Sohl, 1960) may support primitive status for a round profile. If the adapically carinate "*Turritella humerosa* group" is not very closely related to the other lower Tertiary Coastal Plain species, it could have inherited its whorl shape from a Cretaceous ancestor (perhaps the adapically carinate Cretaceous species of *Torquesia* discussed by Douvillé (1929) and Marwick (1957a)).

Apical and Pleural Angles and Shell Geometry

Although formal generative parameters, such as those of Raup (1966) or Schindel (1990), represent the most thorough method of representing the geometric form of the gastropod shell, apical and pleural angles (Text-figure 8) provide a close proxy for several of the most important geometric aspects, especially in a relatively simple shell such as a turritellid. It is possible that a comprehensive study of formal geometric parameters in these or other turritellids would yield systematically useful data at the species level or above. No such analysis has yet been attempted. Use of apical and pleural angles in the present study has corroborated Merriam's (1941, p.34) opinion that these characters are useful only at the species level.

Size

Since size in many organisms is apparently highly responsive to local selective conditions (Calder, 1984; Stanley, 1985; LaBarbera, 1986), it is of limited value as a taxonomic character. Turritellids exhibit a range of adult sizes from 15 mm total height to more than 300 mm. Modal values for all species, fossil and Recent, however, seem to be between 50 and 100 mm.

Whether size increase predominates over size decrease in the phylogeny of the group generally ("Cope's Rule") is not known. Among Coastal Plain species, larger species tend to be more heavily sculptured than smaller species and on this basis could be seen as more derived. Stanley (1973) has argued that larger species tend to be more specialized than smaller relatives, and tend not to give rise to smaller descendants but rather to become extinct without issue. See Allmon (1994) for a further discussion of the significance of size in Coastal Plain turritellids.

Adult Sculpture

Compared to many other gastropod groups, external shell sculpture in Turritellidae is not well developed. It consists chiefly of spiral cords, ribs, or carinae of various number and strength. Axial elements are rare and of minor importance, but they do occur over the history of the group. The Venezuelan Miocene species *Turritella zuliana* Hodson, 1926, for example, shows pronounced scalloping on its flared anterior carina. A number of species, notably including Cretaceous forms placed in the genus *Torquesia* Douvillé, 1929 as well as the Recent western Atlantic species *Torcula exoleta* (Linnaeus, 1758) show faint to pronounced noding or beading on the spiral ribs of late whorls.

There does not seem to be an overall polarity or trend in sculpture development for Turritellidae as a group over its entire history, although the extremely carinate morphologies typical of many of the larger species in the lower Tertiary of the Coastal Plain are absent from among Recent turritellids (Allmon *et al.,* 1990). Individual lineages, however, do seem to show minor patterns. The beaded Cretaceous species placed by Douvillé (1929) in his genus *Torquesia,* for example, may have been ancestral to unbeaded but similarly adapically carinate Lower Tertiary species in Eurasia as well as the western hemisphere (Rutsch, 1943; Marwick, 1957a).

BIOGEOGRAPHIC CONTROL

A major problem in any phylogenetic analysis is distinguishing between evolutionary and purely biogeographic events (*e.g.,* Eldredge, 1977; Schankler, 1981). Taxa showing first appearances in a region may have recently arisen from *in situ* ancestors, or may have immigrated from elsewhere. This is a particular problem in analyses of a portion of a diverse, widespread and long-lived group such as Turritellidae.

A good way to deal with the possibility of such immigration events would be to carry out phylogenetic studies on related species in likely source areas in order to judge the likelihood that they could have contributed immigrants. Such work has simply not been carried out for turritellids which, despite receiving substantial attention from many authors over many years, remain poorly- to completly unknown in most areas of the world. Even in those areas that have been studied more intensively, the detail is usually insufficient to judge accurately the possibility of immigration to North America at particular. For example, of the three most likely source areas for immigrants into the U.S. Gulf and Atlantic Coastal Plain region in the lower Tertiary—western Europe and the Mediterranean, northern South America and the Caribbean, and the Pacific coast of North America—only in the last region have lower Tertiary turritellids been studied in detail in the last 70 years.

The most recent work on European lower Tertiary species (Cossmann, 1912; Glibert, 1973) does not describe sculptural ontogeny in any detail, and so despite the likelihood (based on overall biogeographic patterns) that Europe and southeastern North America exchanged benthic marine taxa during the early Tertiary, data presently available are insufficient to investigate this possibility for turritellids.[1]

Adegoke (1977) has reported on a probably Late Paleocene macrofauna from Nigeria, discussing turritellids at some length, and describing a new genus, *Reymentella.* His data are summarized in Table 4. Even in this case, when information is available on the apical ontogeny of some species, data are insufficient to judge possible affinities with U.S. Coastal Plain taxa. *Torquesia adabionensis* (Oppenheim, 1915) from Nigeria, for example, is very similar in whorl profile and adult sculpture to "*Turritella*" *humerosa* Conrad from beds of probably similar age in Maryland, but the apical ontogeny of neither species is definitely known. Growth lines of the African species generally agree with those of American species. Of the Paleocene African species with known apical ontogenies, *Haustator nigeriensis* Adegoke, 1977 is somewhat similar to both *Turritella* (herein *Palmerella*) *alveata* Conrad and *T.* (herein *Haustator*) *perdita* Conrad from the U.S. Coastal Plain, but these species are both of Late Eocene age. (It is interesting to note that protoconchs of the three Nigerian species for which they are available appear to be small and multispiral, suggestive of a long planktonic phase and potentailly high dispersal capability.)

The most detailed works on South American Ter-

[1] Preliminary examination of collections in the Institut Royale des Sciences Naturelle de Belgique in Brussels in early 1992 revealed a number of forms from the French, German and Belgian Tertiary that bear considerable outward similarity to Paleogene Coastal Plain species. Detailed study of these forms, particularly SEM examination of their apices, will be required before these very cursory impressions can be verified or rejected.

Table 4.—Character states for Paleocene turritelline species from Nigeria, described by Adegoke (1977).

Species	*apical spiral formula*	*growth line type*	*whorl profile*	*no. whorls in protoconch*
Torquesia adabionensis (Oppenheim, 1915)	?	2A	AC	?
Torquesia oppenheimi Adegoke, 1977	C_1 B_2 A_3 ?	2B	AC	?
Haustator furoni Adegoke, 1977	C_1 B_2 A_3	2A	R	4–5
Haustator nigeriensis Adegoke, 1977	C_1 B_1 A_1*	2A	BC	4–5
Haustator oyawoyei Adegoke, 1977	C_1 B_2 A_3 ?	2A	R-BC	?
Reymentella olaniyani Adegoke, 1977	D_1 C_1 B_1 A_1 R_1 ?**	2B	BC	3

* "All three primary spirals develop in close succession on the 4th to 5th whorls and remain subequal throughout ontogeny; order of appearance of spirals not determined." (Adegoke, 1977, p. 95).
** "Five spirals appear almost simultaneously on the third spire whorl, they represent r, a, b, c, and d (?)" (Adegoke, 1977, p. 98).

tiary turritellids are those of Spieker (1922) and Hodson (1926), but in neither paper are apical sculpture patterns discussed in any detail. Numerous scattered references have been made in the literature to Caribbean and South American turritellid species that seem to be closely related to Paleogene species from the Gulf Coastal Plain. These include forms from the Paleocene Maria Farinha Formation in Pernambuco, Brazil (Gardner, 1931, 1935; Woodring, 1972), and the Paleocene Soldado Formation of Trinidad (Maury, 1912, 1929; Rutsch, 1943; Woodring, 1972).

Macsotay and Scherer (1972) have summarized morphological data on Oligocene-Recent turritellids from the Caribbean and northern South America, and the results of a numerical taxonomic (*i.e.,* phenetic) analysis. Although they present information on "sculpture of the first post-nuclear whorls" in the form of presence/absence of "medial," "posterior," "anterior" or "double" spiral keels, there is insufficient evidence that what is herein referred to as apical spiral ontogeny was in fact observed in all cases. Nevertheless, their study represents a major attempt at a phylogenetic analysis of turritellids, and provides numerous hypotheses for testing. Apical ontogenetic formulae for species as given by Macsotay and Scherer are summarized in Table 5. Based on these data, it appears possible that some lineages of Gulf and Atlantic Coastal Plain turritellids experienced exchange with some or all of the proto-Caribbean basin in the early Tertiary. The paucity of possible relatives outside the Coastal Plain, however, suggests that this interchange may have been in the form of emmigration to the south, rather than immigration into the U.S. Coastal Plain.

Merriam (1941) describes Cretaceous to Recent turritellid species from the Pacific coast in detail, but his information on apical ontogeny is not very useful because, as discussed above, he uses the ambiguous descriptive "uni-, bi- and tricarinate" system. Table 6 summarizes the principal shell characters of the 12 "stocks" identified by Merriam, and his suggestions as to possible affinities with species on the Gulf Coastal Plain. This information is crude, but suggests that members of the "*Turritella*" *humerosa* group on the Gulf and Atlantic Coastal Plains, and perhaps members of the *Turritella* (herein *Palmerella*) *creola* group on the Gulf Coastal Plain (*e.g., T. alveata* Conrad; see discussion of lineages below), could have been Pacific immigrants rather than evolved *in situ.* As discussed in more detail below, these conclusions are consistent with other arguments that the *humerosa* group may not be closely related to other Coastal Plain species.

Short of the ideal specific phylogenetic information that one would like to have, some very general paleogeographic and paleobiogeographic information is available that may give rough indications of times of high immigration into the southeastern U.S. As summarized in Allmon (1990), in the early Tertiary, North America (including Greenland) and Europe were still essentially continuous, allowing not only land mammals to be freely exchanged (McKenna, 1975), but also probably benthic marine invertebrates with no or only short planktonic phases (Berggren and Hollister, 1974, p.150). Molluscan faunas from the Danian of West Greenland, for example, contain several bivalve species comparable to species from the Paleocene Aquia Formation of Maryland and the Thanetian of the Paris Basin (Rosenkrantz, 1970, p.447). According to Kollmann and Peel (1983, pp.43–44), however, West Greenland Paleocene turritellids show closer affinities to European than to American forms.

Davies *et al.* (1975, p.128) have suggested that the Paleocene Midwayan Stage faunas of the Gulf coast show greater similarities to the faunas of northwestern Europe than to those in lower latitudes. Gardner (1931, 1935), on the other hand, emphasizes the Tethyan affiniites of the Midwayan faunas. Middle Eocene molluscan faunas on the two sides of the North Atlantic show both similarities and differences. Assessing the magnitude of each is hindered by lack of reliable sys-

Table 5.—Inferred apical spiral sculpture formulas for Caribbean Neogene turritellid species based on data presented by Macsotay and Scherer (1972). It is unlikely that all of these inferred formulae actually represent earliest sculpture ontogeny, but most probably represent the condition of at least relatively early teleoconch sculpture.

Species	*inferred apical sculpture formula*	Species	*inferred apical sculpture formula*
abrupta Spieker, 1922	ABC_1	*forresti* Brown, 1913	ABC
acropora Dall, 1889	AB_1C	*galvesia* Olsson, 1931	AB_1C
alowensis F. Hodson, 1926	ABC	*gatunensis taratarana* F. Hodson, 1926	AB_1C_1
altilira Conrad, 1857a	ABC_1	*g. gatunensis* Conrad, 1985b	AB_1C_1
a. guppyi Cossmann, 1909	AB_1C	*g. caronensis* Mansfield, 1925	AB_1C_1
a. mirandana F. Hodson, 1926	ABC_1	*gaweaveri* F. Hodson, 1926	AB_1C
a. urumacoensis F. Hodson, 1926	ABC_1	*gilbertharrisi* F. Hodson, 1926	ABC_1
alturana Spieker, 1922	AB_1C	*hubbardi* F. Hodson, 1926	ABC
amaras Woodring, 1957	A_1BC_1	*illesca* Olsson, 1931	ABC
andreasi Williston, in Hodson, 1926	ABC	*infracarinata* Grzybowski, 1899	A_1BC_1
anguillana Cooke, 1919	AB_1C	*larensis* F. Hodson, 1926	AB_1C
bayovarensis Olsson, 1932	AB_1C	*limonensis* Olsson, 1922	AB_1C
berjadinensis F. Hodson, 1926	AB_1C	*lloydsmithi* Pilsbry and Brown, 1917	AB_1C_1
bifastigata Nelson, 1870	AB_1C	*machapoorensis* Maury, 1925	AB_1C
b. cartagenensis Brown and Pilsbry, 1917	AB_1C	*m. wiedenmayeri* F. Hodson, 1926	AB_1C
b. oreodoxa Olsson, 1922	AB_1C	*m. guarirensis* F. Hodson, 1926	AB_1C
buchivacoana F. Hodson, 1926	AB_1C_1	*m. paraguanensis* F. Hodson, 1926	AB_1C
b. canonensis F. Hodson, 1926	AB_1C_1	*maiquetiana* Weisbord, 1962	AB_1C
b. colinensis F. Hodson, 1926	AB_1C	*masasensis* Marks, 1951	ABC
b. warfieldi F. Hodson, 1926	AB_1C	*matarucana* F. Hodson, 1926	ABC
b. socorroensis F. Hodson, 1926	AB_1C	*mauryae* F. Hodson, 1926	AB_1C
b. cocoditana F. Hodson, 1926	AB_1C	*meroensis* Olsson, 1931	A_1BC_1
caleta Olsson, 1931	A_1BC_1	*mimetes* Brown and Pilsbry, 1917	AB_1C
caparonis Maury, 1925	AB_1C_1	*montanitensis* F. Hodson, 1926	AB_1C
cauredalitoensis F. Hodson, 1926	ABC	*perattenuata* Heilprin, 1887	AB_1C
chipolana Dall, 1982	A_1BC_1	*planigyrata* Guppy, 1867	AB_1C
chiriquiensis Olsson, 1922	AB_1C	*praecellens* Brown and Pilsbry, 1917	ABC_1
columbiana Weisbord, 1929	AB_1C_1	*prenuncia* Spieker, 1922	ABC
conquistadorana Hanna & Israelsky, 1925	ABC	*subgrundifera* Dall, 1892	ABC
cornellana F. Hodson, 1926	AB_1C	*systiolata* Dall, 1915	ABC
costaricensis Olsson, 1922	AB_1C	*varicosta* Spieker, 1922	AB_1C
crocus Cooke, 1919	ABC_1	*variegata* Linnaeus, 1758	AB_1C
cruziana Olsson, 1932	ABC	*variegata paraguanensis* F. Hodson, 1926	AB_1C
curamichatensis F. Hodson, 1926	AB_1C	*venezuelana* F. Hodson, 1926	AB_1C
domingensis Brown and Pilsbry, 1917	AB_1C	*v. quirosana* F. Hodson, 1926	ABC
elemensis F. Hodson, 1926	AB_1C_1	*vistana* F. Hodson, 1926	AB_1C_1
falconensis F. Hodson, 1926	ABC_1	*v. nicholsi* F. Hodson, 1926	AB_1C_1
fica Olsson, 1932	A_1BC_1	*zuliana* F. Hodson, 1926	AB_1C
filicarmenensis F. Hodson, 1926	AB_1C		

tematic revisions of even the more important groups. The introduction of molluscan species from Europe to the U.S. Gulf coast may have increased through the Late Eocene, peaking at or around the Eocene-Oligocene boundary (Dockery, 1984). The U.S Gulf coast may well have had more in common with northwestern Europe than with the Tethys-proto Caribbean realm, and only intermittent contact with the Pacific coast of North America (Palmer, 1957, 1967; Davies *et al.*, 1975, p.130; Keen, 1976; Allmon, 1990, pp. 118–119; Nicol, 1991; Givens, 1989).

For the purposes of the following analyses I have assumed that most of the lower Tertiary Coastal Plain species discussed here are not themselves immigrants, nor are they the immediate descendants of such immigrants. Indications of Pacific coast affinities for some taxa are consistent with other data that are independent of biogeographic evidence, as discussed below. Suggestions of relationships to species from the Caribbean and South America (*e.g.*, Macsotay and Scherer, 1972) and Europe (*e.g.*, Glibert, 1973; pers. obs.) also need to be studied in greater detail. This is clearly not an optimal situation. As I have emphasized, data on turritellids from beyond North America are severely lim-

Table 6.—Character states for Cretaceous and Cenozoic turritelline species from California, described by Merriam (1941).

Stock	*age*	*lateral sinus*[1]	*apical sculpture*[2]	*whorl profile*[3]	*possible gulf coast relative(s)*[4]
broderipiana d'Orbigny, 1840	M Mio-Rec	4b	mesocostate	Q	
cooperi Carpenter, 1864	L Mio-Rec	2c	cingulate	U	
ocoyana Conrad, 1857a	M-L Mio	4b	tricostate	Z	
altilira Conrad, 1857b	E Mio-Rec	2b	tricostate	U	*Torcula* spp.
uvasana Conrad, 1855	E Eoc-Rec	2b	bicostate (B_1 C_2 ?)	C	*P. alveata* (Conrad)
buwaldana Dickerson, 1916	E-L Eoc	?	tricostate	C	
andersoni Dickerson, 1916	E-L Eoc	2b	tricostate	H-L	
merriami Dickerson, 1913	E-M Eoc	2b	bicostate (B_1 C_2 ?)	X	"*T.*" *praecincta* Conrad ?
reversa Waring, 1917	Pal-M Eoc	2b	tricostate	X	"*T.*" *humerosa* Conrad
pachecoensis Stanton, 1896	L Cret-Pal	2a	tricostate	J-Y	
chicoensis Gabb, 1864	L Cret	1b	bicostate? (B_1 C_2 ?)	C	*T. vertebroides* Morton
tolenasensis Merriam, 1941	L Cret	1a	tricostate	J	

[1] Lateral sinus type designations after lettered types in Text-figure 10.
[2] "Bicostate" and "tricostate" as explained in text. "mesocostate": "in early ontogeny a more or less median primary, which exists as a carina or angulation in adolescent stages, often later becoming obsolete" (Merriam, 1941, p. 6).
[3] Whorl profile type designations after lettered types in Text-figure 13.
[4] Suggested relationships are Merriam's (1941, pp. 38–43).

ited, and as a result these biogeographic conclusions can serve as no more than hypotheses for future testing.

ANALYSIS OF COASTAL PLAIN SPECIES

Taxa Considered

The following discussion concentrates on those turritellid species most closely related to two common, conspicuous and historically important forms, "*Turritella mortoni* Conrad, 1830" and "*Turritella humerosa* Conrad, 1835b", and is restricted to Paleocene and Eocene occurrences (Tables 7–9).

Recognition of Species Groups

Species related to "*Turritella mortoni* Conrad" and "*Turritella humerosa* Conrad" are recognized by their possessing characters shown by these two forms and lacking in all or most other species. Principal characters and character states for the Paleocene and Eocene Coastal Plain turritellid species that share such characters are given in Table 9. Based on these data and the foregoing discussion of character analysis, four species groups or lineages can be recognized on the basis of shared derived characters. These are referred to below as the "*mortoni* group", the "*creola* group", the "*rina* group", and the "*humerosa* group".

Relationships Among Species Groups: a Cladistic Approach

In attempting a cladistic analysis of these species, the first and in many ways most difficult decision is the choice of an outgroup. Eldredge (1979, p.171) has emphasized that there is no hard and fast rule governing the selection of the correct outgroup for comparison with the taxa of interest. The method of outgroup comparison should be viewed rather as a continuous procedure of pair-wise comparison. Potential sister groups are proposed on the basis of previous or independent phylogenetic information and analysis, and alternatives are tested by how well they accord with available data.

At this point in the study of Turritellidae, so little detailed morphological documentation and phylogenetic analysis have been done that there is no guarantee that any named group chosen as an outgroup (*e.g.*, a supraspecific taxon from Europe or the Pacific coast of North America) will, when combined with the Coastal Plain taxa of interest, comprise a monophyletic, or at least not polyphyletic, group. 2) There are no corroborated hypotheses of possible evolutionary relationships between these lower Tertiary species and particular Cretaceous forms from the Coastal Plain or elsewhere. Those links that have been proposed (*e.g.*, Merriam, 1941; Marwick, 1957a; Sohl, 1960, p.71) are based on little more than similar whorl profile.

For these reasons, I have chosen to use hypothetical outgroups in the following analyses. This avoids having to wait for taxa in other areas and times to be examined in detail before Coastal Plain species can be considered at all. The number of relevant characters is low and can easily be specified for a variety of outgroups; these character lists can then be used at a later date to test relationships between actual monophyletic taxa and these coastal plain species.

Three alternative cladograms for the relationship

Table 7.—Described species of turritellid gastropods (excluding species assigned to the genus *Mesalia* Gray, 1842) from the Paleocene and Eocene of the U.S. and their taxonomic placement in the present paper. * indicates species for which well-preserved shell apices are known. Names in brackets are not recognized as separate taxa in the present paper.

"*Turritella mortoni* Group" (placed in *Palmerella* n. gen.)
- *alabamiensis* Whitfield, 1865*
- *alveata* Conrad in Wailes, 1854*
- *apita* de Gregorio, 1890*
- *arenicola* (Conrad, 1865)*
- [*a. branneri* Harris, 1891]
- [*a. danvillensis* Stenzel and Turner, 1940*]
- *chirena* Stenzel and Turner, 1940*
- *clevelandia* Harris, 1892*
- *creola* Palmer in Harris and Palmer, 1947*
- *dumblei* Harris, 1895a*
- *dutexata* Harris, 1895a*
- *femina* Stenzel in Renick and Stenzel, 1931*
- [*f. oligoploka* Stenzel in Renick and Stenzel, 1931]
- *hilli* Gardner, 1935
- *levicunea* Harris, 1896
- *lisbonensis* Bowles, 1939
- *mortoni mediavia* Bowles, 1939
- *mortoni mortoni* Conrad, 1830*
- *pleboides* (Vaughan, 1895)*
- *mortoni postmortoni* Harris, 1894a
- *potomacensis* Clark and Martin, 1901
- *mortoni* "*premortoni*" Govoni, 1983 (Govoni and Hansen, in press)*
- *stenzeli* Allmon, n. sp.

"*Turritella rina* Group" (placed in *Haustator* Montfort, 1810)
- *carinata* I.Lea, 1833*
- [*carina palmerae* Bowles, 1939]
- *cortezi* Bowles, 1939
- *fischeri* Palmer in Richards and Palmer, 1953
- *gilberti* Bowles, 1939*
- *infans* Stenzel and Turner, 1940*
- *martinensis* Dall, 1892
- *perdita* Conrad, 1865*
- [*perdita jacksonensis* Cooke, 1926*]
- [*perdita lowei* Cooke, 1926*]
- *rina* Palmer, 1937*
- [*rina carolina* Palmer, 1937]
- [*rina wechesensis* Bowles, 1939]
- *rivurbana* Cooke, 1926
- *subrina* Palmer, 1937
- *subtilis* Kellum, 1926
- *tennesseensis* Gabb, 1860*
- *vaughani* Bowles, 1939

"*Turritella humerosa* Group" (placed in "*Turritella*")
- *aldrichi* Bowles, 1939*
- *biboracesis* Gardner, 1945
- *claytonensis* Bowles, 1939
- *eurynome* Whitfield, 1865
- *gardnerae* LeBlanc, 1942
- *humerosa* Conrad, 1835b*
- *multilira* Whitfield, 1865
- *praecincta praecincta* Conrad, 1864*
- *praecincta virginiensis* Allmon, n. ssp.
- "*prehumerosa*" Govoni, 1983 (Govoni and Hansen, in press)*
- *toulmini* Allmon, n. sp.

Incertae Sedis
- *bunkerhillensis* Palmer in Harris and Palmer, 1947
- *dobyensis* Dockery, 1980*
- *kincaidensis* Plummer, 1933
- *mcbeanensis* Bowles, 1939
- *mingoensis* Bowles, 1939
- *nasuta* Gabb, 1860*
- [*n. brazita* Stenzel and Turner, 1940]
- [*n. felli* Bowles, 1939]
- [*n. houstonia* Harris, 1895]
- [*n. smithvillensis* Bowles, 1939]
- *nerinexa* Harris, 1895a
- *obruta* Conrad, 1833
- *ola* Plummer, 1933
- *plummeri* Stenzel and Turner, 1940
- *polysticha* Stenzel and Turner, 1940
- *saffordi* Gabb, 1860
- *turneri* Plummer, 1933*

among species groups in these Paleogene Coastal Plain species are shown in Text-figure 14. Several points concerning these cladograms are important:

1) Outgroups in the three cladograms differ only in their whorl profile (*i.e.,* "round," "basally carinate" and "adapically carinate"). This is consistent with the foregoing discussions and the data summarized in Tables 1 and 9 that suggest that the closest relatives of the Coastal Plain species had an apical sculpture formula of C_1 B_2 A_3, a *hybrida-imbricataria*-type lateral growth line aspect, a moderately deep basal sinus, and a moderate size and apical angle. These character states are therefore presumed to be plesiomorphic in the Coastal Plain species.

2) These cladograms are based on the weighting scheme described above, without which many other arrangements would be equally plausible. For example, if apical ontogeny and whorl profile were weighted equally and an outgroup with a round whorl profile were used, the *creola* group would be primitive rather than derived, and the C_1 B_2 A_3 apical sculpture formula of the *rina* group would be derived (and homoplastic) rather than primitive.

3) The only synapomorphic character possibly uniting all Coastal Plain species in a monophyletic group is the lack of beaded sculpture. This character change is proposed very tentatively and only because many Cretaceous species, particularly in Eurasia, bear such sculpture prominently (*e.g.,* Douvillé, 1929) and some of the lower Tertiary Coastal Plain species vestigially. Given the uncertainty of the Cretaceous ancestry of Coastal Plain species, however, this is a very difficult hypothesis to support at the present time. Even if the ancestry were more definite, loss characters are gen-

Table 8.—Geographic range and stratigraphic duration of Paleocene and Eocene turritelline species from the U.S. Gulf and Atlantic Coastal Plains.

Ranges were calculated by connecting the geographic centers of counties containing one or more reported occurrences of the species with straight lines, forming maximum area convex polygons, and measuring the enclosed areas with an electronic digitizing tablet. Exceptions were made to allow for the known shape of the Lower Tertiary shoreline and continental shelf edge (*i.e.*, ranges were not calculated over area presumed to be land or continental slope; using the paleogeographic interpretations of Murray [1961], Rainwater [1964], Toulmin [1977], Breard [1978], Siesser [1984b], Hansen [1987] and Dockery [1988]). Species known from only two localities are given ranges equal to the distance between the two in km^2. Species known from single localities, or from multiple localities within a single county, are arbitrarily given ranges of 10 km^2. Ranges are given for time slices defined by correlative lithostratigraphic units across the Coastal Plain; for species known from more than one such temporal unit, ranges are given for each unit individually.

Duration is the estimated total lifetime of a species over the entire interval of deposition of all stratigraphic units in which it occurs, and so are maximum estimates given the known stratigraphic distribution. Values were calculated based on best available biostratigraphic dates for formational boundaries, using the absolute timescale of Berggren *et al.* (1985).

Abbreviations of lithostratigraphic units: AQ, Aquia Formation; BA, Bashi Marl; BM, Black Mingo Group; BS, Brightseat Formation; CH, Castle Hayne Limestone; CL, Clayton Formation; CM, Cook Mountain Formation; DBT, Doby's Bluff Tongue; GS, Gosport Sand; KI, Kincaid Formation; LL, Lower Lisbon Formation; LO, "Logansport Formation" (=Lime Hill); MB, Moodys Branch Formation; MCB, McBean Formation; MLM, Matthews Landing Marl Member of Porters Creek Formation; MR, Marthaville Formation; NA, Naheola Formation; NF, Nanafalia Formation; PC, Porters Creek Formation; PE, Pendleton Formation; QC, Queen City Formation; RK, Reklaw Formation; SCB, Stone City Beds; SR, Shark River Formation; TS, Tuscahoma Formation; TSBL, Bells Landing Marl Member of Tuscahoma; TSGL, Greggs Landing Marl Member of Tuscahoma; UL, Upper Lisbon Formation; WB, White Bluff Formation; WE, Weches Formation; WP, Wills Point Formation; YZ, Yazoo Formation.

Species	*time unit*	*range (km²)*	*duration (my)*	Species	*time unit*	*range (km²)*	*duration (my)*
alabamiensis	NA	10	7.6	*levicunea*	NA	10	7.6
	WP-PC	66			PC	10	
	KI-CL	404,054		*lisbonensis*	CM-UL-MCB	248,239	6.0
aldrichi	LO-NA	679	7.6	*mcbeanensis*	MCB	10	3.0
	WP-PC	66		*mingoensis*	BM	10	3.0
	KI-CL	9,122		*mortoni mortoni*	AQ	2,092	3.2
alveata	MB-WB	63,965	0.5	*multilira*	MR-NF	4,338	2.6
apita	GS	10	0.3	*nasuta*	CM-UL-MCB	206,987	13
arenicola	YZ	205	7.7	*nerinexa*	WE	57,086	4.0
	MB-WB	146,785		*obruta*	GS	10	0.3
carinata	GS	50	5.0	*ola*	KI	10	4.0
	CM-UL	74,160		*perdita*	MB	37,526	0.5
chirena	WE	10	3.0	*pleboides*	CM	64	3.0
claytonensis	CL	208	4.0	*polysticha*	WP	10	1.0
clevelandia	YZ	201	7.0	*mortoni postmortoni*	PE-TS	39,990	3.2
	MB	45,350			MR-NF	45,832	
cortezi	CM	45,832	2.0	*potomacensis*	AQ	2,092	3.2
creola	MB	2,196	0.5	*praecincta praecincta*	PE-TS	39,714	5.8
dobyensis	DBT	10	1.0	*praecincta virginiensis*	AQ	2,092	3.2
dumblei	CM	8,306	3.0	"*prehumerosa*"	BS	10	1.5
dutexata	CM	122,794	3.0	*mortoni* "*premortoni*"	BS	10	1.5
eurynome	PE-TS	14,443	5.8	*rina*	CM-UL-MCB	130,581	7.0
	MR-NF	890		*rivurbana*	MB	7,453	0.3
femina	WE	65	3.0	*saffordi*	CL	1,446	4.0
	BA	10		*stenzeli*	KI	42	4.0
gilberti	BA	35,523	3.2	*subrina*	CM-UL-MCB	123,016	7.0
hilli	KI	10	4.2	*subtilis*	CH	10	5.0
houstonia	CM	20,172	3.0	*tennesseensis*	CL	13,720	4.0
humerosa	AQ	2,092	3.2	*toulmini*	CL	10	4.0
infans	CM	37	3.0	*turneri*	QC	10	3.0
	SCB	10			RK	622	
kincaidensis	KI	346	4.2	*vaughani*	MCB	10	2.0

erally undesirable because of the high chance of homoplasy (*cf.*, Hecht, 1976).

4) It seems likely that the species of the *humerosa* group are not particularly closely related to the other Coastal Plain species, for the following reasons:

i) possible relationships between the *humerosa* group and turritellid species from elsewhere are more supported than for the other Coastal Plain species groups (*e.g.*, Merriam (1941) for the Pacific coast, Rutsch (1943) for the Caribbean and South America); ii) as

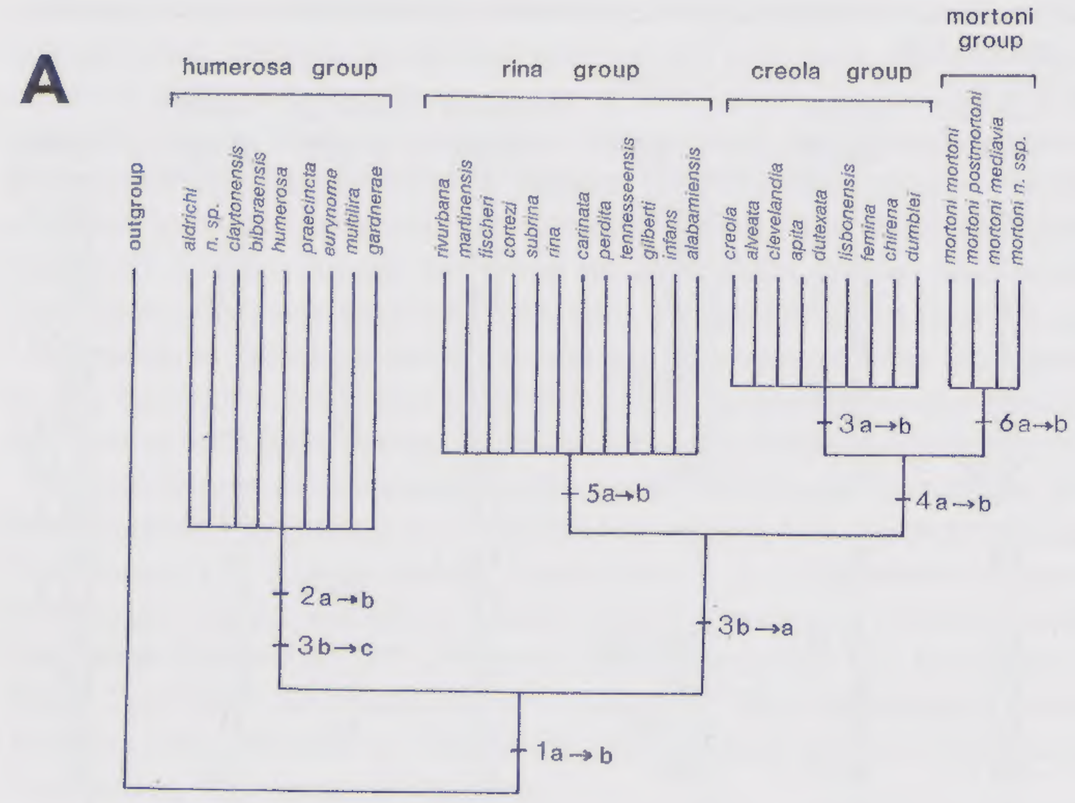
Table 9.—Character states for Paleocene and Eocene turritellid species from the Gulf and Atlantic Coastal Plains discussed in this paper. Conventions and abbreviations as in Table 1.

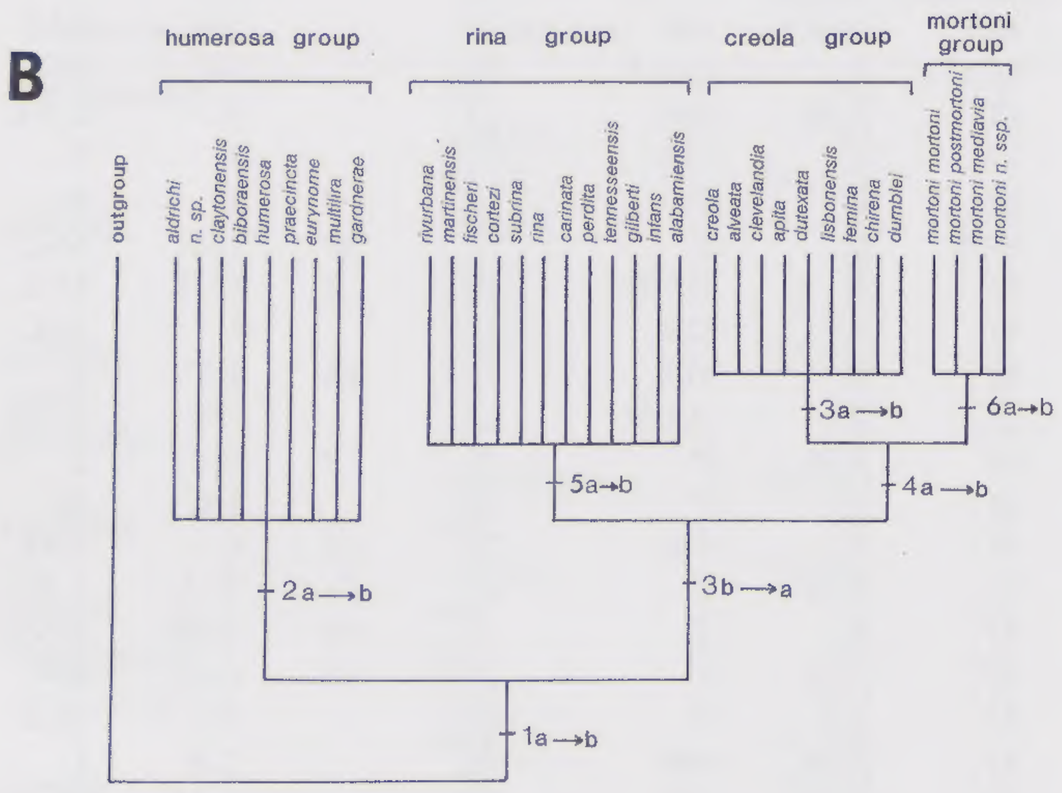
Species	*apical sculpture formula*	*growth line*					*apical angle*	*pleural angle*	*whorl profile*	*size*
		basal sinus	*type*	*lateral depth*	*sinus apex*	*angle*				
alabamiensis	C1 B2 A3	4	2	M	B	OR-P	20		J	M
aldrichi	C1 B2 A3	4–5	2	M	B	OR	14		Q	M
alveata	C1 B1 A2	3–4	2	M	A-B	OR	18		D	M
apita	C1 B1 A2	3	2	M	B	OR	20		V	S-M
arenicola	C1 B1 A2	3–4	2	M	A-B	OR-P	25	20	C	M
carinata	C1 B2 A3	4	2	M	B	P	15	19	J-L	M-L
chirena	C1 B1 A2	4	2	S-M	B	OR	27		J	S-M
claytonensis	?	?					19		Q-X	M-L
clevelandia	C1 B1 A2	4–6	2	M	B	P	16		J	M
cortezi	?	?					16	27	U	M-L
creola	C1 B1 A2	3	1–2	M	A-B	OR-OP	22		C	M
dobyensis	C2 B1 A3	3	2	M	B	OR	15	12	C	M
dumblei	C1 B1 A2	4–5	2	M	B	P-OR	17	17	J	M
dutexata	C1 B1 A2	?	1	M	A-B	OR	21		C-J	M
eurynome	?	6?	2	M	B	P	14		Q-X	L
femina	C1 B1 A2	2–3	1–2	M	B	P-OR	23		C-J	M
gilberti	C1 B2 A3	4–5	1	M	A-B	OR	20		D-J	S-M
hilli	?	4	2	M-D	B	OR-P	20		J-Y	M-L
humerosa	C1 B2 A3	3	2	M	A-B	OR	17		X	L-VL
infans	C1 B2 A3	3	1–2	M	A	OR	19		J	S
kincaidensis	?	4–6	2	M	B	P	15		J	M
levicunea	?	4	2	S-M	B	P	22	30	H-L	M-L
lisbonensis	?	3	2	M	B	P-OR	19	7	C-D	M-L
martinensis	C1 B3 A2 ? (1)	?	2	M	B	OR	14		L	M-L
mortoni mediavia	?	4	2	M	B	OR	21	23	J-Y	L
mortoni mortoni	C1 B1 A2	4	2	M	B	P-OR	22		J-Y	L-VL
multilira	?	3	2	M	A-B	P	16	9	X-Q	L
perdita	C1 B2 A3	3–4	3?	M	B	P	16		J-D	M
pleboides	C1 B2 A3	3	1	M	A	OR	20	18	C	S-M
mortoni postmortoni	?	4	1–2	M	A-B	P	23	21	Y-Z	L-VL
praecincta	?	4–6	2	M	B	P	19	14	X-W	L-VL
prehumerosa	C1 B2 A3 (2)	?	2	M	A-B	P	17	15	Q-X	M-L
mortoni "premortoni"	C1 B2 A3/C1 B1 A2 (3)	4	2	M	B-C	P	22		J-Y	M-L
rina	C1 B2 A3	4	2	M	A-B	OR	18		L-Y	L
rivurbana	?	4–5	2	M	A-B	OR	16		L-U	M
stenzeli	?	4	1	M	A	OR	17		J-U	M
subrina	?	4	2	M	B	OR	23		U	L
tennesseensis	C1 B2 A3	?	2–3	M	B	OR-P	17		U	S-M
toulmini	?	3	2	M	B	OR	10		X-C	M-L

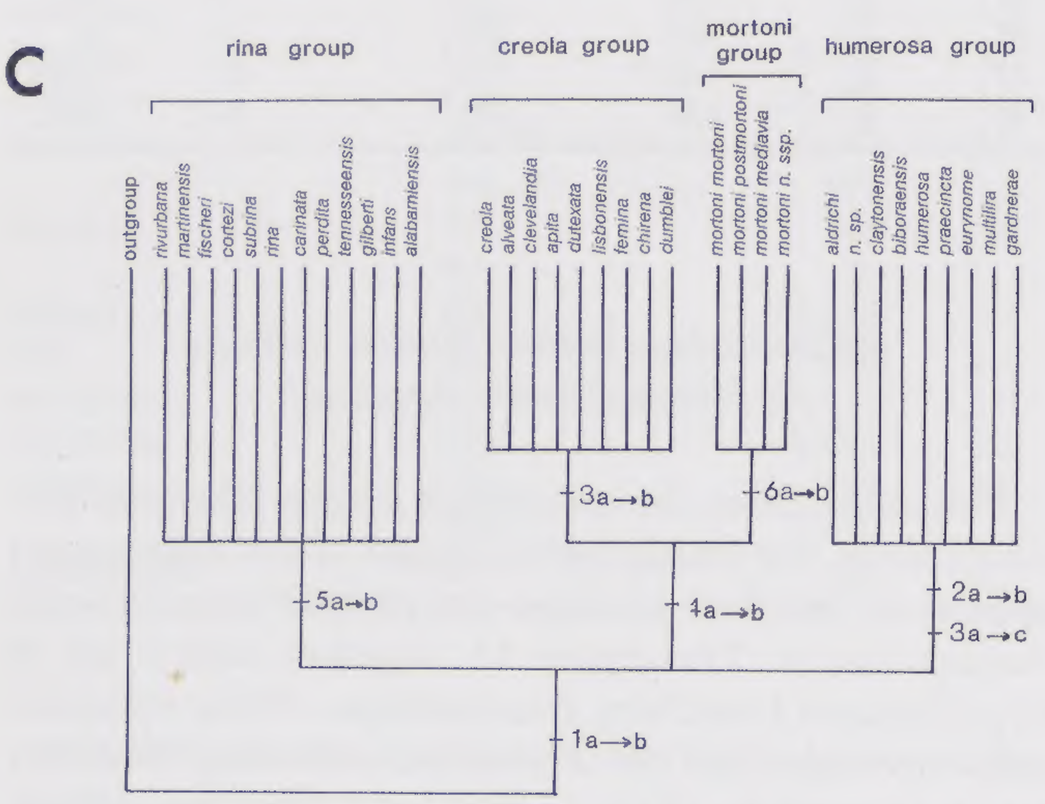
already mentioned, Spiller (1977) states that "*Turritella*" *humerosa* has a multispiral protoconch, suggestive of a more extended planktonic phase and higher potential for dispersal, and this may have allowed more contact with regions outside the Coastal Plain; iii) the adapically carinate whorl profile of the *humerosa* group would not appear to be morphogenetically very close to the basally carinate profile of the *rina* group, with which the *humerosa* group shared a common apical sculpture formula; it seems more reasonable to assume that if these two lineages are related at all, that they developed their distinct whorl profiles independently from a noncarinate ancestor.

Relationships within Species Groups: a Stratophenetic Approach

Following from the discussion in the Methods section above, the stratigraphic ranges of the component species of the four lineages are plotted on an evolutionary tree in Text-figure 15, together with a set of hypothesized branching relationships. These relationships are based on stratophenetic reasoning (Bretsky, 1979; Gingerich, 1979; Lazarus and Prothero, 1984): morphologically similar species found in close geographic and stratigraphic proximity are assumed to be closely related. Exact branching order within a cluster







Text-figure 14.—Three alternative cladograms showing possible relationships of four of the principal species groups of turritellid gastropods from Paleocene and Eocene sediments of the U.S. Gulf and Atlantic Coastal Plains. These cladograms differ only in the nature of the outgroup, which is hypothetical in each case. **A**. Outgroup with beaded sculpture, paucispiral protoconch, $C_1B_2A_3$ apical sculpture formula, and round whorl profile. **B**. Outgroup with beaded sculpture, paucispiral protoconch, $C_1B_2A_3$ apical sculpture formula, and adapically carinate whorl profile. **C**. Outgroup with beaded sculpture, paucispiral protoconch, $C_1B_2A_3$ apical sculpture formula, and basally carinate whorl profile. See text for further discussion. Characters and character states are as follows: 1. beaded sculpture, a. present, b. absent; 2. protoconch, a. paucispiral, b. multispiral; 3. whorl profile, a. basally carinate, b. round, c. adapically carinate; 4. apical sculpture formula, a. $C_1B_2A_3$, b. $C_1B_1A_2$; 5. strength of B spiral in adults, a. well developed, b. weak to absent; 6. strength of C spiral, a. moderate, b. very strong to carinate. Cladogram 1 or 2 is preferred based on likely form of Cretaceous ancestor (i.e., outgroup) and probability that humerosa group is only distantly related to other Coastal Plain clades (i.e., that similarities are shared primitive characters). See text for further discussion.

of such species is determined by the balance among the three variables of morphology, stratigraphy and geography. For example, of three species in the same area and stratigraphic horizon, the two sharing the most similarities are assumed to be more closely related; of three equally dissimilar species, the two occurring closest in either time or space are most closely related.

Individual supraspecific relationships based on this stratophenetic approach are discussed in the systematic section below.

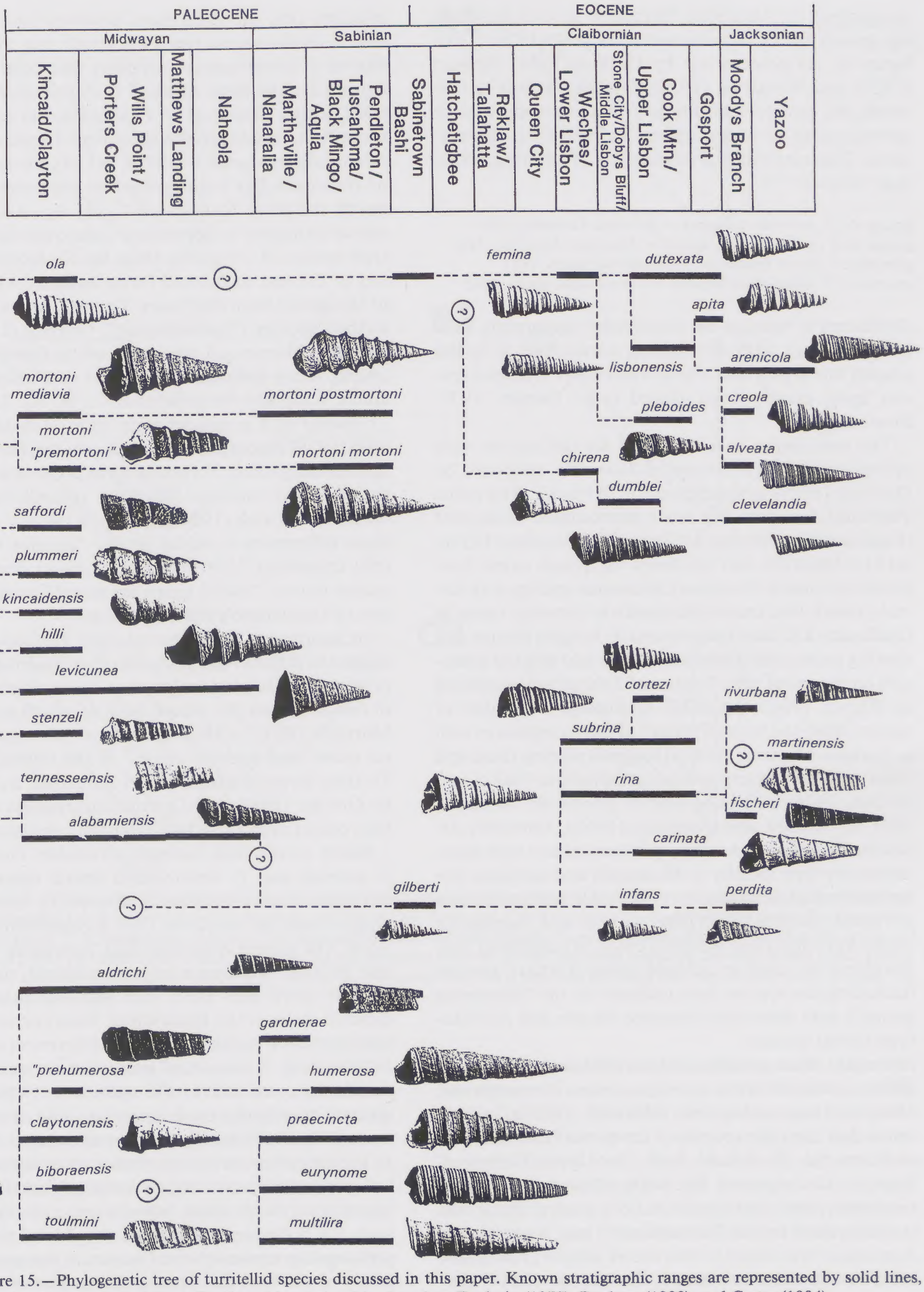
Supraspecific Taxa in the Present Study

A persistent pattern in the literature on North American Cenozoic turritellids is the reluctance of investigators to assign species to formal supraspecific groups. Palmer (1937), for example, while noting that "The Claibornian species do not belong to *Turritella* s.s. according to the lines of growth," uses the name *Turritella* "in the broad sense of the genus." The reasons for this reluctance are summed up by Merriam (1941, p.35):

> According to the standards of taxonomy herein proposed, the European and austral genera, subgenera and sections could be evaluated only by study of complete and well-preserved "genotype" material. This has been done for only one or two of these. Until this study is accomplished for all, it is considered inexpedient to propose additional generic or subgeneric names, or, in America at least, to attempt to use most of those already existent.

Allison and Adegoke (1969, p.1250) similarly state that "Much additional study of *earliest apical ontogeny* is yet necessary before Bowles' [1939] groups can be reconstituted naturally. Until this information is available, formal nomenclature should not be provided for his groupings as they now stand" (emphasis in original).

The only commonly discussed basis for suprageneric



Text-figure 15.—Phylogenetic tree of turritellid species discussed in this paper. Known stratigraphic ranges are represented by solid lines, inferred relationships by dashed lines. Stratigraphic relationships based on Toulmin (1977), Dockery (1980), and Carter (1984).

assignment of American Paleogene species has been the growth line classification of Guillaume (1924) (Text-figure 9). As pointed out by Dollfus (1926), Stewart (1927) and Woodring (1928), Guillaume fails to correlate his groups with already existing supraspecific names, some of which appear to match his descriptions. The conventional pairing (*e.g.,* Woodring, 1928) is as follows:

groupe de *T. terebralis* Lamarck = *Turritella* Lamarck, 1799
groupe de *T. imbricataria* Lamarck = *Haustator* Montfort, 1810
groupe de *T. turris* Basterot = *Archimediella* Sacco, 1895
groupe de *T. subangulata* Brocchi = *Torculoidella* Sacco, 1895

Guillaume's "groupe de *T. hybrida*" apparently does not match up with an existing name, and it is this growth line group into which American Paleogene species have usually been placed (*e.g.,* Palmer, 1937; Bowles, 1939).

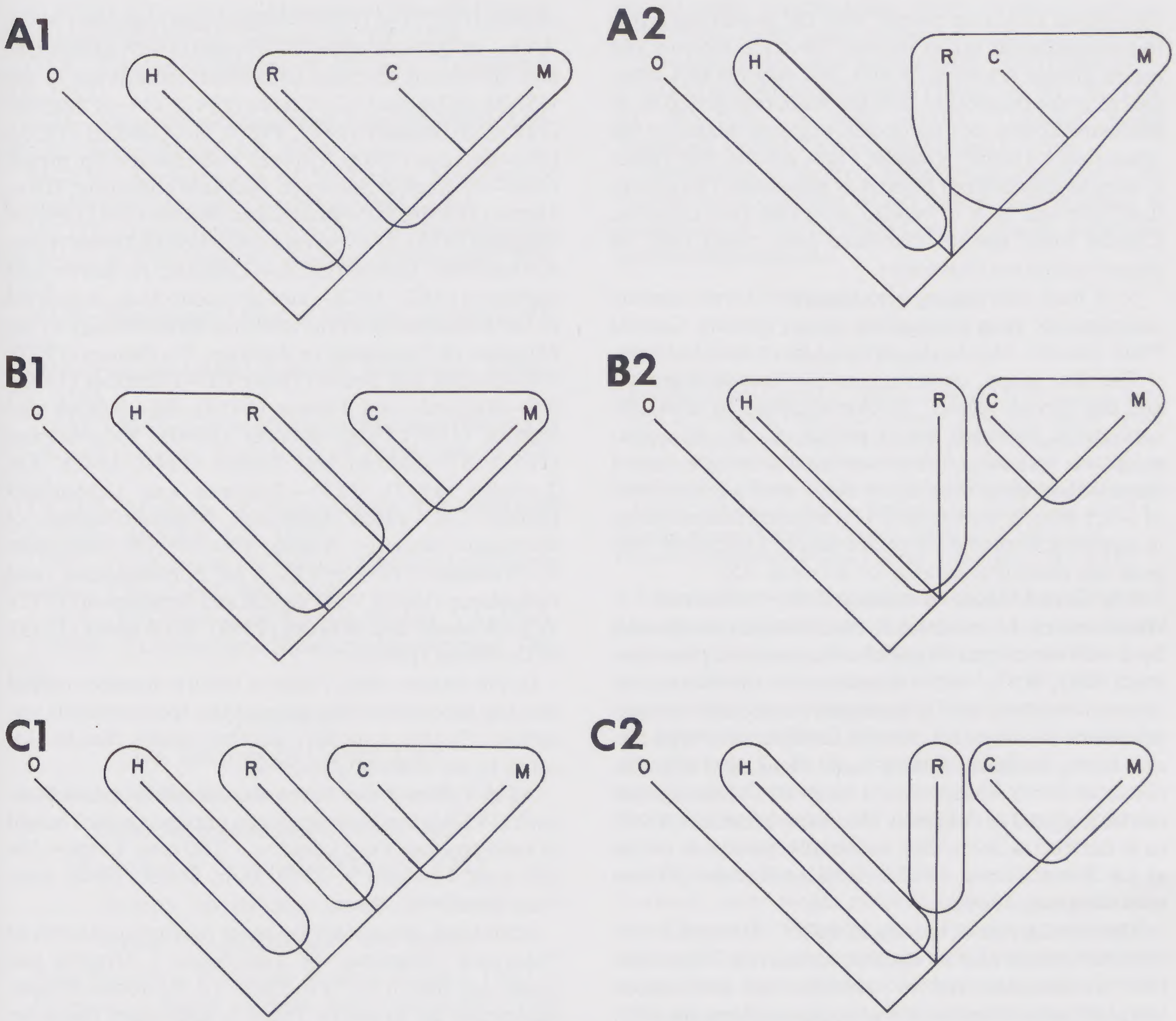
The only name ever proposed for the species with *hybrida*-type lateral sinuses is *Turricula,* proposed by Douvillé (1929) as a subgenus of *Turritella.* The name *Turricula,* however, is a much preoccupied name, and is unavailable (Bowles, 1939, p.270; Marwick, 1957a, p.161). Douvillé also proposes the genus name *Torquesia* to contain Eurasian Cretaceous species with lateral growth line traces intermediate between those of Guillaume's *T. imbricataria* and *T. hybrida* groups and bearing prominent adapical carinae and beaded sculpture on the spiral ribs. The use of *Torquesia* is extended by Rutsch (1943, pp.163ff) to include a number of species from the lower Tertiary of the Americas as well as Eurasia. Marwick (1957a) suggests placing these and other similar Tertiary species in *Ispharina* Vialov and Soloun, 1936, as a subgenus of *Torquesia.* As made clear by Allison and Adegoke (1969), however, *Ispharina* is a *nomen nudum,* because neither type specimens nor type locality is designated and adequate descriptions and illustrations of the type species are not provided. Govoni (1983) and Govoni and Hansen (in press) have followed Rutsch (1943) in suggesting that *Torquesia* be used to include lower Tertiary species (including the species here included in the "*humerosa* group") with adapically carinate whorls and *hybrida*-type lateral sinuses.

Despite these opinions, I believe that the described differences between the nominate genera *Torquesia* and *Haustator* are ambiguous. Marwick (1957a, p.154) states that the type species of the genus *Haustator, H. imbricatarius* (Lamarck) from the Upper Eocene of England, has a growth line with a "moderately deep, moderately oblique lateral sinus of a general shape that is widespread in the Turritellinae", and suggests that homoplasy was likely in this rather simple growth line type. As already mentioned, Guillaume (1924) emphasizes that the differences between his *T. hybrida* and *T. imbricataria* types are small; my own examination of these species supports this opinion (Text-figure 12). The basal sinus of *T. imbricataria* is somewhat deeper than that of *T. hybrida,* but even this is somewhat variable in the specimens I have examined. According to Marwick (1957a, p.154), the type species of *Haustator* has a three-whorled protoconch and an apical sculpture formula of C_1 B_2 A_3. Although the apical ontogeny is apparently unknown for both the type species of *Torquesia* from the Cretaceous and for any of the less sculptured forms assigned by Marwick to the genus from the lower Tertiary, an as yet undescribed species ("*prehumerosa*" Govoni (1983); Govoni and Hansen, in press) placed by Govoni in *Torquesia,* has a protoconch of about two whorls and an apical sculpture formula of d C_1 B_2 A_3. In erecting *Torquesia* as a genus separate from *Haustator,* Douvillé (1929) places most emphasis on the whorl profile; species assigned to *Torquesia* have prominent adapical carinae while those in *Haustator* typically have basal carinae. Marwick (1957a, p.160), however, states that these differences in whorl profile "are not taxonomically important." Nevertheless, Marwick declares *Torquesia* to be a "useful genus for many Cretaceous species of Guillaume's *hybrida* group."

In summary, *Torquesia* s.s. and *Haustator* do not appear to differ in any features other than the presence or absence of beaded sculpture and the vertical position of carination on the whorl, both of which are features Marwick (1957, p.160) declares to be "apparently of no more than specific value." If the unbeaded lower Tertiary forms are included in *Torquesia,* as suggested by Govoni (1983) and Govoni and Hansen (in press), then one of even these two diagnostic characters is lost.

Based on the data currently available, Guilllaume's *T. hybrida* and *T. imbricataria* lateral sinus types do not appear to be sufficiently discrete or non-overlapping criteria on which to base supraspecific designations. The genera *Haustator* and *Torquesia,* therefore, can be said to share a common lateral sinus form. Further work may show that some of these species differ in form of the basal sinus. Data currently available, however, indicate that such differences are minor.

The genus *Torquesia,* if it is to be recognized at all, should be restricted to the species for which it was erected: the chiefly Eurasian, adapically carinate Cretaceous species bearing prominent beaded sculpture. In the lower Tertiary of the western hemisphere, adapically carinate species largely lacking beaded sculpture, but sharing the *hybrida-imbricataria* growth line type (*e.g.,* "*T.*" *humerosa* Conrad) should be placed in a genus-group separate from *Torquesia.* It is possible that many of the Eurasian species discussed under *Isphar-*



Text-figure 16.—Three possible supraspecific classifications of Paleocene and Eocene Coastal Plain turritellids. Diagrams on the left assume either of cladograms A or B in Text-figure 14; diagrams on right assume cladogram C in Text-figure 14. H = *humerosa* group, R = *rina* group, M = *mortoni* group, C = *creola* group. **A1, A2**. Two supraspecific taxa, one including the *humerosa* group, the other the *mortoni, creola* and *rina* groups. **B1, B2**. Two supraspecific taxa, one including the *humerosa* and *rina* groups, the other including the *mortoni* and *creola* groups. **C1, C2**. Three supraspecific taxa, one including the *humerosa* group, one the *rina* group, and the other the *mortoni* and *creola* groups. This is the scheme adopted here.

ina by Marwick may also belong here. (If it should prove to be the case that *"Turritella" humerosa* has a small, multispiral protoconch suggestive of a long planktonic interval (as indicated by Spiller, 1977), such wide dispersal of this clade would be more likely.)

The choices for supraspecific assignment of the Paleocene and Eocene Coastal Plain species are summarized in Text-figure 16, superimposed on the possible cladograms discussed in the previous section. The three choices are as follows:

1) Based on whorl profile, the *mortoni, rina* and perhaps *creola* species groups could be placed in the genus *Haustator* Montfort (choices 1a and 1b), but this would mean that species with two distinct apical ontogenetic formulae (C_1 B_2 A_3 and C_1 B_1 A_2) would be included in a single genus. As discussed above, most previous work, as well as the present study, indicates that lineages can be recognized on the basis of apical ontogeny.

2) If apical ontogeny is given the most emphasis, the

rina group might be placed with the *humerosa* group in a supraspecific taxon separate from the *mortoni* and *creola* groups (choices 2a and 2b). Against this alternative is the possibility that the *humerosa* group is, as discussed above, not particularly closely related to the other lower Tertiary Coastal Plain species, but rather to similar species from Eurasia or elsewhere. The growth line form and lack of beaded sculpture that unite the Coastal Plain species discussed here could both be shared primitive characters.

3) A final alternative is to recognize three separate supraspecific taxa among the lower Tertiary Coastal Plain species. This is the option I have adopted here.

The first taxon, consisting of the "*mortoni* group" and the "*creola* group," is characterized by a basally carinate to rounded whorl profile, C_1 B_1 A_2 apical sculpture formula, *hybrida-imbricataria*-type lateral sinus, moderately deep basal sinus, and a protoconch of 1–2.5 whorls with small P1. It appears that no name is currently available for such a taxon. I therefore propose the name *Palmerella* for it (see p. 45).

The second taxon, consisting of the "*rina* group," is characterized by prominent basal carination formed by a well developed D spiral, an apical sculpture formula of C_1 B_2 A_3 with a tendency for the B spiral to become obsolete late in ontogeny, especially in later members of the group, *hybrida-imbricataria*-type lateral sinus, moderately deep basal sinus, and a protoconch of 1–2.5 whorls with a small P1. These species can be assigned to the genus *Haustator* Montfort, 1810, as a derived branch that eventually gave rise to the genus *Torcula* Gray, 1847 in the Late Eocene (Allison and Adegoke, 1969).

The third group of species includes "*Turritella*" *humerosa* Conrad and its apparent relatives. These species are characterized by moderate to pronounced adapical carination, an apical sculpture formula of C_1 B_2 A_3, *hybrida-imbricataria*-type lateral sinus, moderately shallow basal sinus, and a protoconch possibly varying from 1–1.5 to 3–4 whorls with a small P1. Information is presently insufficient to assign these species to a formal genus-level taxon with confidence, and I reluctantly follow tradition by assigning it to "*Turritella*" *sensu lato.*

SYSTEMATIC PALEONTOLOGY

In the descriptions that follow, the locality information given represents all locality records known to me for each species. Abbreviations of localities refer to those listed in Appendix 2. At least one source for each record is indicated in the parentheses following the abbreviation.

Abbreviations for these sources are as follows: A—Allison (1965, 1967); AA—Allison and Adegoke (1969); ANS—ANSP collection; B—Bowles (1939) (documentary specimens for most of Bowles' records are in the USNM collection); C—Cooke (1943); CA—Campbell (1992); D-Dockery (1977, 1980); G—Gardner (1935); GO—Govoni (1983), Govoni and Hansen (in press); GSA—Geological Survey of Alabama collection; HA—Harris (1894b); HP—Harris and Palmer (1947); HU—Hughes (1958); JA—private collection of James Allen, Alexandria, Louisiana; L—LeBlanc *in* Barry and LeBlanc (1942); MCZ—author's collection, deposited in the Department of Invertebrate Paleontology of the Museum of Comparative Zoology; P—Palmer (1937); PB—Palmer and Brann (1966); PL—Plummer (1933); RP—Richards and Palmer (1953); RS—Renick and Stenzel (1931); S40—Stenzel (1940); S53—Stenzel (1953); ST—Stenzel and Turner (1940, 1942); T—Toulmin (1977); TLM—Toulmin and LaMoreaux (1963); TX—Texas Memorial Museum/Bureau of Economic Geology, Austin; US—USNM collection; V—Vaughan (1896); VC—Van Nieuwenhuise and Colquhoun (1982); VS—Veatch and Stephenson (1911); WW-Wassem and Wilbert (1943); W-Wilbert (1953); WD—Ward (1985).

In the locality lists, ? after a locality number means that the species identification of the specimen(s) is uncertain. (?) after a locality number means that the locality is not definitely known.

As in Tables 1 and 9, the size classification of Marwick (1971) is used in referring to maximum shell height of each species: Very Large = > 100 mm, Large= 50–100 mm, Medium = 20–50 mm, Small=10–20 mm, Very Small=< 10 mm.

Sculptural ontogenies for most species are shown as "Marwick Diagrams" in Text-figure 7. Growth line traces are shown in Text-figure 12. Protoconch measurements are given in Table 3, and other character states summarized in Table 9.

Measurements given in tables for locality numbers represent *largest* individuals observed from these localities. Apical and pleural angles have been measured on type specimens, unless otherwise indicated.

See Text-figures 3,4,6 and 8 for illustration of morphological terms used in descriptions.

Abbreviations of Repository Institutions

ANSP—Academy of Natural Sciences of Philadelphia, Philadelphia, PA, USA

FGS—Florida Geological Survey type collection; now held at Florida Museum of Natural History, University of Florida, Gainesville, FL, USA

FMNH-UC—Field Museum of Natural History, Chicago, IL, USA

FLMNH-UF—Florida Museum of Natural History, University of Florida, Gainesville, FL, USA

GSA—Geological Survey of Alabama, Tuscaloosa, AL, USA

LSU—Museum of Geoscience, Louisiana State University, Baton Rouge, LA, USA

MCZM—Department of Mollusks, Museum of Comparative Zoology, Cambridge, MA, USA

MCZIP—Department of Invertebrate Paleontology, Museum of Comparative Zoology, Cambridge, MA, USA

MGS—Mississippi Office of Geology, Jackson, MS, USA

PRI—Paleontological Research Institution, Ithaca, NY, USA

TMM/TBEG—Texas Memorial Museum/Bureau of Economic Geology, University of Texas, Austin, TX, USA

UCMP—Museum of Paleontology, University of California, Berkeley, CA, USA

UNC—Department of Geology, University of North Carolina, Chapel Hill, NC, USA

USGS—U.S.Geological Survey, Reston, VA, USA

USNM—U.S.National Museum, Washington, DC, USA

Systematics

Class Gastropoda Cuvier, 1797

Subclass Prosobranchia Milne-Edwards, 1848

Order Mesogastropoda Thiele, 1925

Superfamily Cerithiacea Fleming, 1822

Family Turritellidae Lovén, 1847[2]

Genus **PALMERELLA**, new genus

Type Species.—*Turritella mortoni* Conrad, 1830

Diagnosis.—Small to very large turritellids with round to basally carinate adult whorl profile and apical sculpture formula of C_1 B_1 A_2.

Description.—Shell small to very large, of 10–25 whorls. Protoconch of 1–2.5 whorls with small P1. Apical sculpture formula C_1 B_1 A_2. Profile of adult whorls round to basally carinate. Sculpture consists of multiple simple, moderately developed spiral ribs. Apical angle usually equal to, but occasionally less than, pleural angle. Lateral sinus of the "*hybrida-imbricataria*" type, basal sinus moderately deep and simple.

Stratigraphic and Geographic Distribution.—U.S.Gulf and Atlantic Coastal Plain (VA, NC, SC, GA, AL, MS, LA, TX, AR), Mexico, Trinidad? South America?; Lower Paleocene—Upper Eocene.

Etymology.—Named after Dr. Katherine V.W. Palmer in recognition of her many contributions to knowledge of Coastal Plain fossil mollusks, especially turritellid gastropods.

Palmerella alveata
(Conrad *in* Wailes, 1854)
Plate 5, Figures 7–9

Turritella alveata Conrad *in* Wailes, 1854, pl.17, f.7 (reprint, 1939, pl.4, f.7); Conrad, 1856, p.263 (reprint, 1939, p.9); Harris, 1894b, p.120, 169, 181; Bowles, 1939, p.306, pl.32, f.1; Stenzel and Turner, 1942, card 43; Palmer *in* Harris and Palmer, 1947, p.288, pl.36, f. 7–12; Brann and Kent, 1960, p.897; Allison, 1965, p.671; Palmer and Brann, 1966, p.980; Dockery, 1977, p.44, pl.3, f.5.
Mesalia alveata (Conrad). Conrad, 1865a, p.33; 1866, p.25.
Turritella (*Haustator*) *alveata* Conrad. Cossmann, 1912, p.118.

Description.—Shell medium sized, of 18 to 22 whorls. Maximum observed whorl diameter 12.2 mm. Apical angle 18°; apical and pleural angles approximately equal. Sutures slightly to moderately incised. Protoconch erect, homeostrophic, turbinate, of 0.75–1.0 smooth, rounded, somewhat inflated whorls; P1 small. Apical sculpture formula C_1 B_1 A_2. Primary spirals B and C appearing simultaneously in lower ½ of whorl, abruptly becoming prominent and of equal strength. Primary spiral A appearing within 1.0 whorl on upper ⅓ of whorl, remaining slightly weaker than B and C for 1–2 whorls, after which all primaries of approximately equal strength. Secondaries r, s and t appearing between primaries around whorl 8–9. Teleoconch whorls wider than high. Profile of early teleoconch whorls roughly evenly convex; later whorls rounded and slightly basally convex to straight-sided. Area between C spiral and suture deeply excavated and smoothly concave. Lateral aspect of growth line trace slightly prosocline, with upper and lower inflection points. Lateral sinus moderately deep with apex about at whorl middle. Spiral and basal sinuses roughly symmetrical and relatively shallow.

Measurements.—See Table 10.

[2] The name "Turritellidae" was introduced independently by Clark (1851) and Woodward (1851), with priority usually attributed to Woodward (*e.g.*, Knight, 1960, p.I317). The first use of a formal suprageneric name for the group, however, is apparently that of Lovén (1847, p.194) as "Turritellea". According to Article 11fii, ICZN, "A family-group name of which the latinized suffix is incorrect is available with its original authorship and date, but with a corrected suffix" (ICZN, 1985, p.27), and thus Lovén is the correct authority for the name Turritellidae.

Table 10.—Measurements of *Palmerella alveata* (Conrad). Abbreviations: MD = maximum diameter (including carina if present) in mm., MH = maximum height, in mm., WN = whorl number, to the nearest 0.5.

	MD	*MH*	*WN*
ANSP 13213 lectotype	12.2	48.1	17
ANSP 13213 paratype	11.9	44.5	15.5

Stratigraphic and Geographic Distribution.—MS, LA: Moody's Branch Formation; AR: White Bluff Formation; lower Jacksonian Stage, Upper Eocene.

Type Locality.—Moody's Branch, Jackson, Hinds County, Mississippi (MS-HN-4).

Other Localities.—MS-HN-1b (B), MS-HN-1c (D), MS-HN-1d (B), MS-HN-2 (D), MS-HN-3 (D), MS-HN-4b (B), MS-CL-3 (B), LA-FR-1 (B), LA-GR-1 (B), LA-GR-1a (B), LA-LS-1 (B), LA-CL-1b (D), LA-CL-1c (D), LA-CL-1e (D), LA-CL-1g (D), LA-CL-1h (D), LA-CL-2 (D), LA-CL-3 (D).

Type Material.—lectotype and paratype of *T. alveata* Conrad ANSP 13213.

Remarks/Discussion.—The type specimens are much larger than average for the species; mean height of specimens I have examined is closer to 30–40 mm than to 40–50 mm. In sculpture and whorl profile *Palmerella alveata* is most similar to *P. creola* (Palmer) and *P. arenicola* (Conrad), also from the Moodys Branch Formation. All three of these species show generally rounded whorls, widest in the lower half, and narrow excavated bands just above the suture. *Palmerella alveata* has the least inflated whorls of the three. *P. alveata* often co-occurs with but is less abundant than *Haustator perdita* (Conrad) at most exposures of the Moodys Branch; at Bunker Hill Bluff on the Ouachita River (LA-CL-2) and Riverside Park in Jackson, Mississippi (MS-HN-6), however, *P. alveata* is the most common turritellid and among the most common macrofossils.

Palmerella apita (de Gregorio, 1890)
Plate 4, Figures 6,7

Turritella carinata H.C.Lea, 1841, p.96, pl.1, f.10; 1849, p.107; Meyer, 1887, p.54, pl.3, f.1,1a; Harris, 1895b, p.10; not I.Lea, 1833, p.129.

Turritella apita de Gregorio, 1890, p.123, pl.11, f.8, f.26, copy *T. carinata* H.C.Lea, 1841, f.27a, 27b, copies Meyer, 1887; Cossmann, 1893, p.29; Harris, 1895b, p.82; Palmer, 1937, p.195, pl.24, f.1,3,7,10; *in* Harris and Palmer, 1947, p.285; Bowles, 1939, p.275, pl.31, f.4; Stenzel and Turner, 1942, card 44; Brann and Kent, 1960, p.898; Glibert, 1962, p.103; Allison, 1965, p.672; Palmer and Brann, 1966, p.980–981; Toulmin, 1977, p.301, pl.50, f.2.

Description.—Shell small to medium sized. Maximum observed whorl diameter 10.0 mm. Apical angle 20°; apical and pleural angles approximately equal. Sutures only moderately incised. Protoconch and earliest teleoconch whorls not seen; Palmer (1937, p.196) and Allison (1965, p.672) report an apical sculpture formula of d C_1 B_1 a_2. On earliest whorls examined, primary spiral B quickly becoming most prominent, forming single sharp keel on middle of whorl. C spiral much less prominent and A even less. Whorl profile between C spiral and lower suture relatively straight, sloping evenly inward, and marked by fine, evenly spaced spiral ribs. Lateral aspect of growth line trace orthocline to slightly prosocline with upper and lower points of inflection. Lateral sinus moderately deep with apex at about middle of whorl. Spiral and basal sinuses relatively shallow.

Table 11.—Measurements of *Palmerella apita* (de Gregorio). Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 494978	8.0	26.0	10.5
MCZIP 29290	10.9	24.8	6
MCZIP 29291	8.0	21.8	7.5

Measurements.—See Table 11.

Stratigraphic and Geographic Distribution.—AL: Gosport Sand; GA: McBean Formation[3] (?); LA: Cook Mountain Formation (?); upper Claibornian Stage, Middle Eocene.

Type Locality.—Claiborne Bluff, Alabama River, Monroe County, Alabama (AL-MO-1a).

Other Localities.—AL-CL-4 (MCZ), GA-JO-1 (VS) ?, LA-WI-1 (V) ?

Type Material.—holotype of *T. apita* De Gregorio PRI 26438; lectotype of *T. carinata* H.C.Lea ANSP 13173.

Remarks/Discussion.—I have not been able to confirm records for this species from beds of Cook Mountain age, and for the present consider it to be restricted to the Gosport Sand, in which it is relatively rare. I have not seen a well preserved apex; if the apical sculpture formula given by Palmer (1937) and Allison (1965) is correct, it is another illustration of an apparently "unicarinate" species not being truly so on its earliest whorls (see also *Palmerella arenicola* (Conrad), below). This is in contrast to "*Turritella*" *dobyensis* Dockery, 1980, which appears to be truly unicarinate. Possible phylogenetic relationships of *Palmerella apita* are discussed below under *P. arenicola.*

Palmerella arenicola (Conrad, 1865b)
Plate 5, Figures 3–6

Turritella plebeia Say. Owen, 1860, pl.9, f.6; not Say, 1824, p.125.

Mesalia ? *arenicola* Conrad, 1865b, p.141, pl.10, f.11; 1866, p.11 [locality not Oregon as given].

Turritella carinata I.Lea. Heilprin, 1884, p.37; Call, 1891, p.8; not I. Lea, 1833.

Turritella arenicola (Conrad). Dall, 1891, footnote in Call, 1891, p.8; 1892, p.232,310; Stewart, 1927, p.354; Bowles, 1939, p.275, pl.31, f.5–7; Stenzel and Turner, 1942, card 45; Palmer *in* Harris

[3] The status of the "McBean Formation" is unclear. It is most probably a sandy facies of the upper Claibornian Santee Limestone, and equivalent to the upper part of the Lisbon/Cook Mountain Formation and/or the Gosport Sand in Alabama (see Huddlestun and Hetrick, 1985; Campbell, 1992, 1995; Dockery and Nystrom, 1992; Fallaw and Price, 1992).

and Palmer, 1947, p.281, pl.34, f.8–11; Brann and Kent, 1960, p.898–9; Allison, 1965,p.673–4; Palmer and Brann, 1966, p.981; Dockery, 1977, p.43–4, pl.3, f.16,17; 1980, p.82, pl.56, f.7,8,10 Toulmin,1977, p.335, pl.62, f.12,13.

Turritella arenicola branneri Harris, 1894b, p.169, pl.6, f.7; Schuchert, Dall, Stanton, and Bassler, 1905, p.676; Palmer, 1937, p.197, pl.23, f.1,2; *in* Harris and Palmer, 1947, p.283, pl.34, f.2,3,6,7; Stenzel and Turner, 1942, card 49; Wilbert, 1953, p.123, pl.2, f.5; Brann and Kent, 1960, p.899; Allison, 1965, p.674.

Turritella arenicola danvillensis Stenzel and Turner, 1940, p.841, pl.47, f.4,5; 1942, card 58; Palmer *in* Harris and Palmer, 1947, p.284, pl.34, f.1,4,5, pl.35, f.1; Brann and Kent, 1960, p.899,900; Allison, 1965, p.672–673; Palmer and Brann, 1966, p.981–982.

Description.—Shell medium sized, of 18 to 22 whorls. Maximum observed whorl diameter 12.0 mm. Apical angle 25°; pleural angle sometimes slightly less than apical angle. Sutures only slightly incised. Protoconch erect, homeostrophic, turbinate, of about 2.0 smooth, rounded, somewhat flattened whorls; P1 small. Apical sculpture formula C_1 B_1 A_2. Primary spirals B and C appearing approximately simultaneously as broad prominence at around middle of whorl. B quickly becoming more prominent, forming single, conspicuous, sharp carina on middle of whorl. Primary A appearing shortly after B and C, but remaining faint. B remaining most prominent for up to 10 whorls, after which other primaries and secondaries emerging abruptly, covering upper surface of intermediate and late whorls with numerous, evenly spaced, subequal spirals, changing whorl profile from keeled to rounded and slightly basally convex. B and C becoming equally prominent and the most conspicuous sculptural elements. Area between C spiral and suture widening and becoming slightly concave. Lateral growth line trace generally prominent, usually prosocline, with upper and lower inflection points and relatively shallow lateral sinus; apex just above middle of whorl. Spiral and basal sinuses relatively shallow.

Measurements.—See Table 12.

Stratigraphic and Geographic Distribution.—MS, LA: Moody's Branch Formation, Yazoo Formation (Danville Landing Member); AR: White Bluff Formation; TX, MX: horizon unknown; GA,SC: McBean Formation[4] ?; upper Claibornian ? and Jacksonian Stages, Upper Eocene.

Type Locality.—Garland Creek, Clarke County, Mississippi (MS-CL-3).

Other Localities.—MS-CL-15 (D), MS-CL-18 (D), MS-YZ-4 (B), MS-YZ-5 (B), MS-HN-1 (D), MS-HN-4 (D), LA-GR-1 (B), LA-GR-1d (B), LA-RA-1 (B), LA-RA-2 (B), LA-CL-6 (D), AR-BR-1(B), AR-DR-1 (B), AR-JF-1 (W,US), AR-SF-1 (B), AR-SF-2 (B), AR-SF-4 (B), AR-CL-1b (H), AR-CL-4 (H), AR-CL-8 (H), TX-ST-1 (B), TX-SA-2b (B), MX-TA-1 (B), MX-TA-2 (B), MX-NL-3 (B), GA-BU-1 (VS), GA-JO-1 (VS), SC-O-1 (CA).

[4] See Footnote 3, p.46.

Table 12.—Measurements of *Palmerella arenicola* (Conrad). Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 489002	12.0	41.0	10.5
USNM 495144	9.0	36.0	13.5
MS-YZ-5	10.2	34.2	10
MS-CL-3	10.4	32.3	11
LA-CA-1	10.0	22.9	5

Type Material.—lectotype of *T. arenicola* Conrad ANSP 15536; holotype of *T. a. branneri* Harris USNM 135141; syntypes of *T. a. danvillensis* TMM/TBEG 20962, 20963.

Remarks/Discussion.—Allison (1965, pp.672–3) states that the upper Jacksonian subspecies *Turritella arenicola danvillensis* Stenzel and Turner has an apical sculpture formula of C_1 B_1 A_2 but that *arenicola* s.s. shows C_2 B_1 A_3. I have not see specimens with the latter pattern; the description given above is for specimens from the Moodys Branch Formation in Clarke County, Mississippi, and suggests that both Yazoo and Moodys forms show similar apical ontogenies and belong to a single taxon.

The similar apical sculpture and early strength of the B spiral in *Palmerella apita* (de Gregorio) and *P. arenicola* suggest a close relationship between these two species. The rounded whorl profile and strength of the two lowest spirals on later whorls in *P. arenicola* suggest a relationship with the lineage of *P. femina* (Stenzel), including *P. dutexata* (Harris), and *P. lisbonensis* (Bowles) (see discussion of these forms below). The smaller pleural angle in *arenicola* in particular may indicate relationship with *P. lisbonensis*. *Palmerella apita* and *P. arenicola* may represent descendants of the *femina* lineage in which the B spiral became stronger than the C spiral, this pattern persisting to adulthood in *apita*, and ending much earlier in the ontogeny of *arenicola*.

Palmerella chirena
(Stenzel and Turner, 1940)
Plate 3, Figures 7–9

Turritella chirena Stenzel and Turner, 1940, p.838, pl.47, f.3; 1942, card 54; Palmer and Brann, 1966, p.984.

Description.—Shell small, of 10 to 15 whorls. Maximum observed whorl diameter 7.0 mm. Apical angle 27°; apical and pleural angles approximately equal. Sutures only slightly incised. Teleoconch whorls wider than high. Protoconch suberect, homeostrophic, turbinate, of 2.0–2.5 smooth, rounded whorls; P1 small. Apical sculpture formula C_1 B_1 A_2. Primary spirals B and C appearing approximately simultaneously as faint,

Table 13.—Measurements of *Palmerella chirena* (Stenzel and Turner). Abbreviations as in Table 10.

	MD	*MH*	*WN*
TMM/TBEG 20960 holotype	7.7	19.5	9.5

broad prominence just below middle of whorl. Within 1.0 whorl A appearing very faintly, B and C diverging and profile between C and suture becoming excavated and concave. Shape of early to intermediate teleoconch whorls generally rounded, of late whorls straight-sided and subquadrate. Lateral aspect of growth line trace orthocline, showing only lower point of inflection and relatively shallow lateral sinus whose apex is above whorl middle. Spiral and basal sinuses of moderate depth.

Measurements.—See Table 13.

Stratigraphic and Geographic Distribution.—TX: "Cane River Formation" (see remarks below); Claibornian Stage, Middle Eocene.

Type Locality.—road from Chireno to Hwy. 21, Nacogdoches County, Texas (TX-NA-8).

Other Localities.—TX-NA-7 (MCZ).

Type Material.—holotype of *T. chirena* Stenzel and Turner TMM/TBEG 20960.

Remarks/Discussion.—The stratigraphic position of beds in East Texas identified by Stenzel and Turner as "Cane River" is unclear. The Cane River Formation was named by Spooner (1926) for beds in Louisiana occurring stratigraphically above those of the Wilcox Group and below the Sparta Sand. Ellisor (1929) recognizes the Cane River in the subsurface in East Texas, underlying the Reklaw, and it is so indicated on a USGS correlation chart (Wilmarth, 1930). Eargle (1968) states that the Louisiana Cane River beds correlated with beds of the Weches, Queen City and Reklaw in East Texas. I have not been able to relocate the type locality of *P. chirena* near the town of Chireno; all outcrops in ditches between the town and Highway 21 lack macrofossils. A good outcrop containing fairly well preserved specimens of *P. chirena* (locality TX-NA-7), however, occurs on Hwy. 21, approximately 7 km west of Chireno. Exposed here are approximately 5 m of highly glauconitic, clayey sand containing small to medium sized oysters identifiable as *Cubitostrea smithvillensis* (Harris) and/or *C. lisbonensis* (Harris), both of which are characteristic of the Weches Formation. Lithologic and faunal evidence is therefore consistent with assigning this outcrop and, provisionally at least, the type occurrence of *P. chirena* to the Weches Formation.

Palmerella chirena shares with *P. dumblei* (Harris) from the overlying Stone City and Cook Mountain beds a similar apical sculpture formula and basally carinate whorl shape, but differs in its greater apical angle and somewhat smaller size. Both *P. chirena* and *P. dumblei* may be derived from a form similar to specimens here noted for the first time as occurring in the upper Sabinian Bashi Formation and assigned to *P. femina* (Stenzel) (see p. 51).

The origins of *Palmerella chirena,* and its apparent relative *P. dumblei,* are unclear. These Middle Eocene species share with the Late Paleocene *P. mortoni* (Conrad) the C_1 B_1 A_2 apical sculpture formula and a basally carinate whorl profile, but are much smaller. They share with the Middle-to-Late Eocene species of the "*creola* group" the same apical sculpture formula and relatively modest size (see Text-figures 14,15). Based on size alone, it does not seem likely that *mortoni* was actually ancestral to these forms. There are thus two choices for the origin of *chirena* and *dumblei.* Either they are derived from the "*creola* group," in which case their basally carinate whorl profile is not homologous to that in *mortoni* and its close relatives, or they are derived from a lineage that split off from the "*mortoni* group," probably in the earliest Paleocene, before the time of *P. mortoni mediavia* (Bowles) and *P. mortoni* ssp. ("*premortoni*" Govoni, 1983; see Govoni and Hansen, in press). Based on the reasoning and confidence estimates discussed above, and summarized in Table 2, I favor the former alternative. It seems unlikely that a group arising in the Coastal Plain region in the Early Paleocene would leave no trace until the Middle Eocene. (The alternative view is, however, supported by the previously unreported presence of *P. femina* (Stenzel) from the Bashi Marl of Alabama (see below), which provides a potential Lower Eocene ancestor for the *creola* lineage. It is possible that, because *chirena* and *dumblei* are small, relatively uncommon Texas forms, the somewhat more poorly preserved Paleocene-lowermost Eocene Texas macrofossil record has thusfar concealed their derivation from a *mortoni*-like ancestor.)

The "*creola* group" itself has no definitely known ancestor on the Coastal Plain before the earliest Eocene, and by the argument just given might on these grounds be assumed not to have originated in the region. This may well prove to be the case. It is possible, however, that one of the Early Paleocene species with a round whorl profile (*e.g.,* "*Turritella*" *ola* Plummer, 1933) for which the apical spiral formula is not known might be ancestral to the *creola* lineage, and these should be investigated in addition to seeking possible ancestral forms are sought outside the Coastal Plain.

Palmerella clevelandia (Harris, 1894b)
Plate 5, Figures 1,2

Turritella perdita? Dall, 1891, footnote in Call, 1891, p.8, *fide* Harris, 1894b, p.92.

Turritella mortoni Conrad. Call, 1891, p.8, *fide* Harris, 1894b, p.92; not Conrad, 1830.

Turritella clevelandia Harris, 1894b, p.170, pl.4, f.9; 1899a, p.74 in part [part = *T. gilberti* Bowles]; Vaughan, 1896, p.50; Schuchert, Dall, Stanton and Bassler, 1905, p.676; Palmer, 1937, p.202, pl.26, f.6,7; *in* Harris and Palmer, 1947, p.290, pl.36, f.1–6; Bowles, 1939, p.308, pl.31, f.9,12; Stenzel and Turner, 1942, card 56; Wilbert, 1953, p.123, pl.2, f.4; Brann and Kent, 1960, p.907; Glibert, 1962, p.95; Palmer and Brann, 1966, p.984–5; Dockery, 1977, p.44.

Turritella (*Haustator*) *Clevelandica* [sic] Harris. Cossmann, 1912, p.118.

Description.—Shell small, of 10 to 15 whorls. Maximum observed whorl diameter 5.5 mm. Apical angle 16°; apical and pleural angles approximately equal. Sutures moderately incised. Apical sculpture formula C_1 B_1 A_2. Primary spirals B and C appearing approximately simultaneously just below middle of whorl, of equal strength and beginning to diverge. Primary A appearing within 1.0 whorl, and B becoming more prominent for one to two whorls, after which C becoming slightly more prominent and remains so. Three primaries retaining relative strengths, giving late whorls a tricarinate, subquadrate form. Secondaries present but remaining faint. Lateral growth line trace prosocline with upper and lower inflection points and relatively shallow lateral sinus with apex around whorl middle. Spiral and basal sinuses relatively shallow.

Measurements.—See Table 14.

Stratigraphic and Geographic Distribution.—AR: White Bluff Formation; MS: Moody's Branch Formation; LA: Moody's Branch Formation, Yazoo Formation (Danville Landing Member); TX?, GA?: horizons unknown; Jacksonian Stage, Upper Eocene.

Type Locality.—White Bluff, Arkansas River, Jefferson County, Arkansas (AR-JF-1).

Other Localities.—AR-CL-1b (B), AR-CL-4 (B), AR-CL-4B (B), AR-CL-7 (B), AR-BR-1 (B), AR-SF-1 (B), AR-SF-2 (D), AR-SF-4 (B), MS-YZ-1 (D), MS-YZ-2 (MCZ), LA-GR-1 (JA), LA-CA-1 (HP), LA-CA-2 (HP), GA-JO-1 ? (VS), GA-GL-2 ? (C).

Type Material.—lectotype of *T. clevelandia* Harris USNM 498010, syntypes USNM 135142.

Remarks/Discussion.—This species is relatively rare. In whorl form and adult sculpture it is most similar to *Haustator gilberti* (Bowles), specimens of which were originally identified as *clevelandia,* but the apical sculpture of the two forms is very different. *P. clevelandia* differs from the other Moodys Branch turritellids of similar apical sculpture in its subquadrate whorl profile and three-ribbed adult sculpture. It may be more closely related to small basally carinate forms of Claibornian age, such as *P. chirena* (Stenzel and Turner).

P. clevelandia is one of two Moodys Branch turritellids to occur in the Danville Landing Member of the Yazoo Formation, the other being *P. arenicola* (Conrad). After noting the similarity of *P. dumblei* (Harris) to the Oligocene species "*Turritella*" *carota* MacNeil, MacNeil (*in* MacNeil and Dockery, 1984, p.53) suggests that *carota* may have been derived from *P. clevelandia.*

Table 14.—Measurements of *Palmerella clevelandia* (Harris). Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 498010	5.9	24.1	13.5

Palmerella creola
(Palmer *in* Harris and Palmer, 1947)
Plate 4, Figures 1–5

Turritella creola Palmer *in* Harris and Palmer, 1947, p.286, pl.35, f.2,4,5; Brann and Kent, 1960, p.909; Allison, 1965, p.671–2; Palmer and Brann, 1966, p.985.

Description.—Shell small to medium sized, of 15 to 20 whorls. Maximum observed whorl diameter 10.0 mm. Apical angle 22°; pleural angle may be slightly less than apical angle. Sutures moderately incised. Protoconch erect, homeostrophic, turbinate, of approximately 1.0 smooth, rounded whorls; P1 small. Apical sculpture formula C_1 B_1 A_2. Primary spirals C and B appearing, faintly at first, around or slightly below middle of whorl, quickly becoming prominent. C may be equal in strength or slightly weaker than B. Primary A appearing two to three whorls later, and remaining faint throughout ontogeny. Sculpture of adult whorls consisting of two prominent spirals (B and C) on lower ⅓ of whorl, separated by a slightly weaker secondary (T). Primary A and secondaries above whorl middle approximately equal in strength but weaker than secondary (T). Teleoconch whorls wider than high, evenly rounded and relatively inflated in profile. Whorl profile below C spiral slightly excavated and concave leading to suture. Lateral aspect of growth line trace orthocline with upper and lower inflection points and moderately deep sinus whose apex is above middle of whorl. Spiral and basal sinuses moderately deep.

Measurements.—See Table 15.

Stratigraphic and Geographic Distribution.—LA, TX, MS: Moody's Branch Formation; lower Jacksonian Stage, Upper Eocene.

Table 15.—Measurements of *Palmerella creola* (Palmer). Abbreviations as in Table 10.

	MD	*MH*	*WN*
PRI 4579 holotype	32.3	10.0	11.5
PRI 4580 paratype	25.2	9.8	5

Type Locality.—Montgomery Landing, Red River, Grant Parish, Louisiana (LA-GR-1).

Other Localities.—TX-SA-2b (HP), MS-YZ-2 (MCZ).

Type Material.—holotype of *T. creola* Palmer PRI 4579, paratypes PRI 4577, 4578, 4580.

Remarks/Discussion.—Palmer (*in* Harris and Palmer, 1947) suggests that *P. creola* is most closely related to "the *T. dutexata* Harris stock of the lower Claiborne." In its rounded, convex whorl profile, *creola* most closely resembles *P. femina* (Stenzel), which is close to *dutexata* (see below). Among Moodys Branch species, *creola* is most similar to *P. arenicola* (Conrad) and *P. alveata* (Conrad).

P. creola is most common at its type locality, the now inaccessible outcrop at Montgomery Landing, but it was apparently not even very abundant there. Mr. James Allen of Alexandria, Louisiana kindly made available to me his collection of turritellids from Montgomery. It was, he says, accumulated in approximately 50 collecting trips, but includes only approximately 40 specimens of *P. creola.*

Palmerella dumblei (Harris, 1895a)
Plate 6, Figures 4–6

Turritella dumblei Harris, 1895a, p.81, pl.9, f.7; Kennedy, 1895, p.123,124,127–29; Palmer, 1937, p.202 in part, pl.26, f.11,15, not f.10 [= *T.* sp., *fide* Palmer and Brann, 1966, p.985]; Bowles, 1939, p.303, pl.32, f.9,19; Stenzel and Turner, 1942, card 59; Palmer and Brann, 1966, p.985.

Description.—Shell small to medium sized, of 15 to 20 whorls. Maximum observed whorl diameter 9.7 mm. Apical angle 17°; apical and pleural angles approximately equal. Sutures only slightly incised. Protoconch of approximately 1.75 smooth, rounded whorls; P1 small. Apical sculpture formula C_1 B_1 A_2. Primary spirals B and C appearing abruptly and at equal strength in middle and lower ¼ of whorl, respectively. Primary A slightly weaker, appearing within 0.75 whorl. Lateral whorl profile straight-sided on early whorls, straight-sided to slightly concave on later whorls with whorl base expanding to form a rounded basal carina. Primary spirals relatively reduced on late whorls, combining with secondaries to cover whorl with numerous evenly spaced, fine, subequal spirals. Whorl profile of late whorls slightly concave with a rounded basal carina separated from lower suture by narrow, slightly concave area marked by two to three minor spirals. Lateral aspect of growth line trace orthocline to slightly prosocline with upper and lower inflection points. Lateral sinus relatively shallow with apex at around whorl middle. Spiral and basal sinuses relatively shallow.

Measurements.—See Table 16.

Table 16.—Measurements of *Palmerella dumblei* (Harris). Abbreviations as in Table 10.

	MD	*MH*	*WN*
TMM/TBEG 35661 holotype	8.2	27.3	8.5
TMM/TBEG 35662 paratype	9.65	32.75	10.0
TMM/TBEG 35663 paratype	7.3	25.8	13.0
TMM/TBEG 35663 paratype	6.0	23.0	15.5
TMM/TBEG 35665 paratype	5.25	13.6	5.5
USNM 498003	7.5	26.5	12.5
USNM 498003	8.0	16.5	3.5

Stratigraphic and Geographic Distribution.—TX: Stone City Beds, Cook Mountain Formation (Wheelock Member); middle Claibornian Stage, Middle Eocene.

Type Locality.—"Moseley's Ferry", Stone City Bluff, Brazos River, Burleson County, Texas (TX-BU-1).

Other Localities. TX-AT-2 (B), TX-AT-3 (B), TX-BR-1 (B), TX-RO-11 (B), TX-SA-2d (US).

Type Material.—holotype of *T. dumblei* Harris TMM/TBEG 35661, paratypes TMM/TBEG 35662, 35663 (2 specimens), 35664, 35665.

Remarks/Discussion.—Its apical sculpture places *P. dumblei* in the genus *Palmerella.* Its basally convex whorl profile suggests a closer relationship to *P. clevelandia* (Harris) than to the more evenly rounded-convex forms such as *P. femina* (Stenzel) and *P. creola* (Palmer).

Palmerella dutexata (Harris, 1895a)
Plate 3, Figures 10–12

Turritella dutexata Harris, 1895a, p.82, pl.9, f.8; Palmer, 1937, p.198, in part, pl.26, f.1,2,4,8,9; *in* Harris and Palmer, 1947, p.287; not Bowles, 1939, p.285, pl.31, f.2 [= *P. femina* (Stenzel)]; Stenzel and Turner, 1942, card 60; Brann and Kent, 1960, p.910, in part, Nos. 2910,2911 only, *fide* Palmer and Brann, 1966; Palmer and Brann, 1966, p.986.

Turritella cf. *dutexata* Harris. Palmer and Brann, 1966, p.986.

Description.—Shell small to medium sized, of 10 to 15 whorls. Maximum observed whorl diameter 8.0 mm. Apical angle 21°; apical and pleural angles approximately equal. Sutures only slightly incised. Protoconch erect, homeostrophic, turbinate, of approximately 1.5 smooth, rounded whorls; P1 small. Apical sculpture formula C_1 B_1 A_2. Primary spirals B and C appearing as broad prominence on lower ½ of whorl, quickly diverging and becoming equally prominent. Primary A appearing within two to three whorls but remaining faint throughout ontogeny. D spiral commonly weakly developed on later whorls but other spirals usually absent. Whorl profile above B concave; all teleoconch whorls bicarinate in aspect. Lateral aspect of growth line trace prosocline with upper and lower inflection points and relatively shallow lateral sinus;

Table 17.—Measurements of *Palmerella dutexata* (Harris). Abbreviations as in Table 10.

	MD	*MH*	*WN*
PRI 2912	9.5	26.1	6.5
PRI 2913	6.9	12.0	6.5

apex above whorl middle. Basal sinus not visible on specimens examined.

Measurements.—See Table 17.

Stratigraphic and Geographic Distribution.—TX,LA,MS: Cook Mountain Formation; AL: Upper Lisbon Formation, Gosport Sand ?; upper Claibornian Stage, Middle Eocene.

Type Locality.—Elm Creek, Lee County, Texas (TX-LE-11).

Other Localities.—TX-RO-12 (B), TX-AN-2 (B), TX-AN-3 (B), MS-CL-1 (B), MS-CL-2 (B), MS-CL-5 (B), MS-CL-16 (B), MS-CL-17 (B), MS-NE-10 (B), MS-NE-11 (B), MS-NE-1 (B), MS-NE-2 ? (P), LA-BI-1 (B), LA-BI-2 (B), LA-BI-3 (B), LA-CB-1 (B), LA-JA-2 (ST), LA-WI-1 (B), LA-WI-2 (B), AL-MO-1a ? (P), AL-CL-14 (MCZ).

Type Material.—holotype of *T. dutexata* Harris TMM/TBEG 1974 lost (*fide* Erickson, 1982).

Remarks/Discussion.—See under *P. femina,* below.

Palmerella femina
(Stenzel *in* Renick and Stenzel, 1931)
Plate 3, Figures 3–6

Turritella femina Stenzel *in* Renick and Stenzel, 1931, p.87,89,107 [reference only], pl.6, f.14; Plummer, 1933, p.644,647,815; Palmer, 1937, p.203, pl.26, f.5, copy Stenzel, 1931; Palmer *in* Harris and Palmer, 1947, p.286; Stenzel and Turner, 1940, p.830, pl.46, f.11–13; 1942, card 64; Palmer and Brann, 1966, p.987.

Turritella dutexata Harris. Bowles, 1939, p.285, pl.31, f.2; not *T. dutexata* Harris, 1895a, p.82.

Turritella femina oligoploka Stenzel *in* Stenzel and Turner, 1940, p. 832, pl.46, f.7–10; Stenzel and Turner, 1942, card 88; Palmer and Brann, 1966, p.987.

Description.—Shell medium sized, of 15 to 20 whorls. Maximum observed diameter 12.0 mm. Apical angle 22°; apical and pleural angles approximately equal. Sutures moderately incised. Protoconch erect, homeostrophic, turbinate, of approximately 1.75 smooth, rounded whorls; P1 small. Apical sculpture formula C_1 B_1 A_2. Primary spirals B and C appearing approximately simultaneously just above and just below whorl middle, respectively, moving within 1.0 whorl to about middle and lower ⅓ of whorl, respectively. Primary A appearing within 0.5 whorl of beginning of B and C, equalling C in strength within one to two whorls. Primary spirals commonly bearing beading or minor scalloping on early teleoconch whorls. Secondaries appearing above and below A on later whorls, where A is weaker than B and C. Upper ½ of whorl thus covered by numerous, approximately equally spaced spirals of moderate strength, lower ½ dominated by two primaries lacking associated weaker spirals. Profile of late whorls rounded and evenly convex. Lateral growth line trace prosocline with upper and lower inflection points and relatively shallow lateral sinus; apex around whorl middle. Spiral and basal sinuses very shallow.

Table 18.—Measurements of *Palmerella femina* (Stenzel). Abbreviations as in Table 10.

	MD	*MH*	*WN*
TMM/TBEG 20965 holotype	10.0	23.0	7.5
TMM/TBEG paratype	9.0	29.0	10.0
TMM/TBEG paratype	12.0	36.0	5.5
USNM 139021	11.3	27.3	5.0

Measurements.—See Table 18.

Stratigraphic and Geographic Distribution.—TX: Weches Formation, (Viesca Member); AL, GA: Bashi Formation; upper Sabinian Stage, middle Claibornian Stage, Upper Paleocene—Middle Eocene.

Type Locality.—Cobb Branch, Robertson County, Texas (TX-RO-6).

Other Localities.—TX-RO-12 (US), TX-LO-12 (ST), TX-LO-13 (RS), AL-CO-1 (MCZ), GA-RA-3 (MCZ).

Type Material.—holotype of *T. femina* Stenzel TMM/TBEG 20965, numerous unnumbered paratypes TMM/TBEG; syntypes of *T. femina oligoploka* TMM/TBEG 20969, 20970, 20971, 20972.

Remarks/Discussion.—In their extreme morphological variants, *P. femina* and *P. dutexata* (Harris) are quite distinct. On its largest whorls *dutexata* has fewer prominent spirals, and the lower half of the whorl is dominated by only two; the upper half bears only a few relatively weak lines, and is markedly concave in profile. Although they also show two prominent spiral ribs on the lower half of the whorl, the adult whorls of *femina* characteristically bear numerous additional spirals of equal to slightly lesser strength, and the entire whorl is convex and slightly inflated in profile. There appear to be intermediates between these two extremes, however, represented in part by the subspecies *femina oligoploka* Stenzel and Turner, which has fewer spiral ribs on the upper half of later whorls and a less inflated profile than *femina* s.s. Stenzel and Turner noted that *femina* s.s. and *f. oligoploka* "are end members of a series" of transitional forms. Both taxa have been recognized only in the Weches Formation of Texas, but from adjoining counties. This morphological series, however, can be extended upward to forms usually identified as *Turritella dutexata* Harris from the

Wheelock Member of the Cook Mountain Formation. Many of these specimens show the reduction in spiral ribbing described in *femina oligoploka,* and a less inflated whorl profile. Specimens from the upper Cook Mountain and Upper Lisbon Formations tend to show the extreme reduction of sculpture on the upper whorl and the characteristic concave profile. As noted by Stenzel and Turner, *dutexata* does not occur with either *femina* or *f. oligoploka,* strengthening an hypothesis of evolutionary transition from one to the other.

Below the Weches, the *femina* lineage also appears to be recognizable in specimens I have collected from the upper Sabinian Bashi Formation in eastern Alabama and western Georgia. Although apices are not preserved, these specimens clearly show the distinctive double carina on the lower half of the whorl, and have rounded concave whorl profiles, and thus are clearly distinguishable from the only other turritellid so far reported from the Bashi, *Haustator gilberti* (Bowles). Recognition of these specimens as belonging to *P. femina* helps to fill an important temporal gap in the history of *Palmerella* in the Coastal Plain Paleogene, and shows that at least two lineages survived the apparent crisis for turritellids that seems to have occurred near the end of the period of deposition of the Tuscahoma Formation, when all of the large, characteristic Sabinian turritellid species disappeared.

A Sabinian representative of the lineage leading to *femina* also may make the search for Paleocene Coastal Plain ancestors more fruitful. The only form currently recognized that may fill this role is "*Turritella*" *ola* Plummer from the Lower Paleocene Clayton Formation of Texas. This species shows two strong carinae on the lower half of the whorl, and a rounded, convex whorl profile. Unfortunately, it is known from only a single specimen from a locality that seems to have disappeared.

The only feature that calls into doubt the relationship of *Palmerella femina* to other Coastal Plain turritellid species is the form of its basal growth line trace, which shows a very shallow sinus. The basal sinus of *P. dutexata* (Harris) is unfortunately not visible on any of the specimens I have examined. The basal sinus on the closely related form *P. lisbonensis* (Bowles), as well as that of *P. pleboides* (Vaughan), however, are similarly shallow. Whether this is sufficient to separate these forms at a high level from other upper Claiborne and Jackson species (*e.g., P. creola* (Palmer), *P. apita* (de Gregorio), etc.), which have deeper basal sinuses, is not clear. Some indication that it is not is provided by the basal sinus of *Haustator perdita* (Conrad), which varies from nearly as shallow to nearly as deep as the extremes shown by these other species.

The evolutionary relationships among *Palmerella femina* (Stenzel), *P. dutexata* (Harris) and *P. lisbonensis* (Bowles) are uncertain. The very shallow to almost straight basal sinus of *P. femina* may call into question its relationship to any other Coastal Plain species. It is, however, very similar in its sculpture to *dutexata* and *lisbonensis,* all three species having pronounced B and C spirals and relatively reduced A spirals throughout ontogeny. It therefore seems likely that *dutexata* is the direct phyletic descendant of *femina,* with *lisbonensis* branching off from this lineage.

Palmerella hilli (Gardner, 1935)
Plate 11, Figure 8

Turritella levicunea Harris. Plummer, 1933, p.815, pl.10, f.4,4a; not *T. mortoni levicunea* Harris, 1896.
Turritella hilli Gardner, 1935, p.292, pl.25, f.4–6; Bowles, 1939, p.301; Stenzel and Turner, 1942, card 68; Palmer and Brann, 1966, p.989.

Description.—Shell medium sized, of perhaps 15 to 20 whorls. Maximum observed whorl diameter 14.0 mm. Apical angle 20°; pleural angle usually slightly greater than apical angle. Protoconch and early apical whorls unknown. Smallest whorls examined showing three spirals of approximately equal strength, spaced equally over the whorl and separated by single smaller spirals. All these spirals becoming reduced in strength on following whorls except lowermost, which increases in strength and forms sharp, flaring basal carina. Additional, anterior rib expanding to equal this spiral, thickening and rounding the carina on last 4–5 whorls. Area between this spiral and the suture on latest whorls becoming slightly convex. Profile of early whorls more or less straight, of later whorls markedly concave as the carina increases in strength. Spirals finely beaded by the intersection of the growth lines with the fine spiral ribs. Lateral aspect of growth line trace orthocline, with upper and lower inflection points and a deep sinus with apex above whorl midpoint. Antispiral and basal sinuses moderately deep.

Measurements.—See Table 19.

Stratigraphic and Geographic Distribution.—TX:

Table 19.—Measurements of *Palmerella hilli* (Gardner). Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 337054 holotype	13.0	35.9	8.5
USNM 12112	13.9	27.2	3.5
USNM 12112	13.4	25.8	3.5
USNM 12112	11.2	31.5	9.0
USNM 12112	12.4	34.9	7.0
USNM 12112	11.3	31.1	8.5

Kincaid Formation; lower Midwayan Stage, Lower Paleocene.

Type Locality.—approx. 1 km above mouth of Dry Creek, Colorado River, Bastrop County, Texas (TX-BA-2b).

Other Localities.—TX-BA-1c (B), TX-BA-15 (B).

Type Material.—holotype and 2 paratypes of *T. hilli* Gardner USNM 337054.

Remarks/Discussion.—Without giving the size of the whorls, Gardner (1935) states that "Early apical whorls sculptured with 2 strong simple spirals on the anterior half of the whorls, another of almost equal strength a little behind the middle and except on the very earliest whorls, a finer spiral directly in front of the posterior suture." Although the apical sculpture is unknown, the sculpture described by Gardner on the earliest known whorls is consistent with a formula of C_1 B_1 A_2 such as shown by *P. mortoni* (Conrad). The adult whorl profile and sculpture of *P. hilli* are also similar to that of *P. mortoni,* although *hilli* is substantially smaller. Govoni (1983) and Govoni and Hansen (in press) state that an undescribed form ("*premortoni,*" *P. mortoni* ssp. herein, see p.64), which they describe from the Brightseat Formation of Maryland (apparently equivalent to part of the Kincaid Formation in Texas), is very similar to *P. hilli.* They note that the Brightseat form "differs from [*hilli*] in details of relative strength and position of the primary spirals in the juvenile whorls and in having a more rounded and slightly less prominent basal carina."

Palmerella levicunea (Harris, 1896)
Plate 11, Figure 4

Turritella mortoni var. *levicunea* Harris, 1896, p.110, pl.11, f.9; Brann and Kent, 1960, p.928; not *T. levicunea* Plummer, 1933, p.815, pl.10, f.4,4a [= *Palmerella hilli* (Gardner)]; not *T. mortoni* Conrad, 1830.

Turritella levicunea Harris. Bowles, 1939, p.301; Stenzel and Turner, 1942, card 74, f.1,9; Palmer and Brann, 1966, p.992–3; Toulmin, 1977, p.174, pl.8, f.9.

Description.—Shell medium sized to large, of perhaps 10 to 15 whorls. Maximum observed whorl diameter 38.0 mm. Apical angle 22°; pleural angle 30°. Sutures generally inconspicuous. Protoconch and earliest teleoconch whorls unknown. Sculpture on earliest known whorls consisting of three moderately prominent spirals, one in approximately the middle of upper ⅓ of whorl, one in middle of lower ⅓, and one very close to lower suture. Upper and middle spirals separated from each other by at least two finer spirals; upper spiral from suture and middle from lower by only one. Upper two spirals decreasing in strength on succeeding whorls as additional intercalary spirals appear, sculpture of later whorls consisting of numerous, more or less evenly spaced, very fine spirals. Lowermost spiral expanding to form edge of sharp basal carina, in earlier whorls just above suture but in later whorls separated from suture by narrow, slightly concave to straight-sided area. Lateral aspect of growth line trace prosocline with indistinct upper and lower inflection points and moderately deep sinus whose apex is just above whorl middle. Antispiral and basal sinuses relatively shallow.

Table 20.—Measurements of *Palmerella levicunea* (Harris). Abbreviations as in Table 10.

	MD	*MH*	*WN*
PRI 43 holotype	18.0	36.0	7.5
USNM 15145	27.6	60.1	7.0
MCZIP 29277	20.0	37.6	8.5

Measurements.—See Table 20.

Stratigraphic and Geographic Distribution.—AL: Clayton Formation, Porters Creek Formation (Matthews Landing Member), Naheola Formation; Midwayan Stage, Lower Paleocene.

Type Locality.—Dale Branch, near Oak Hill, Wilcox County, Alabama (AL-WI-12).

Other Localities.—AL-WI-9 (B), AL-WI-13 (MCZ), AL-WI-53 (T), AL-WI-54 (T), AL-WI-59 (ST).

Type Material.—holotype of *T. levicunea* Harris PRI 43.

Remarks/Discussion.—This species is very rare, the USNM collections containing only 14 specimens, and my own collections only a single specimen from Matthews Landing (MCZIP 29277). The species is, however, highly distinctive in its earlier whorls for its smooth shell surface and large apical and pleural angles. In later ontogenetic stages as space begins to open up between the carina and the lower suture, it begins to resemble *Palmerella mortoni* (Conrad) more closely. In the absence of more knowledge of the apical sculpture, it is assigned only tentatively to *Palmerella*; the basal carina of this species could ally it to either *Palmerella* or *Haustator.*

Palmerella lisbonensis (Bowles, 1939)
Plate 3, Figures 1,2

Turritella nasuta Gabb. Palmer, 1937, p.200, in part, pl.25, f.3,9; Brann and Kent, 1960, p.928, in part, Nos. 2901, 2905, fide Palmer and Brann, 1966, p.993; not Gabb, 1860, p.385.

Turritella lisbonensis Bowles, 1939, p.287, pl.31, f.1,3; Palmer and Brann, 1966, p.993; Toulmin, 1977, p.303, pl.51, f.7.

Turritella dutexata lisbonensis Bowles. Stenzel and Turner, 1942, card 75.

Table 21.—Measurements of *Palmerella lisbonensis* (Bowles). Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 498009 holotype	8.5	39.5	13.5

Description.—Shell medium sized to large, of probably 20 to 25 whorls. Maximum observed whorl diameter 14.2 mm. Apical angle 19°; pleural angle 7°. Protoconch and earliest teleoconch whorls unknown. Earliest whorls examined (dia. = 2.5 mm) bear four spiral ribs, two very prominent of approximately equal strength on lower half, two very weak of approximately equal strength on upper ⅓. Additional weaker spirals appearing above, between and below the two lower primaries, which decrease in strength until whorl is covered by numerous, subequal spirals, approximately equally spaced. Whorl profile changing from basally bicarinate to slightly convex, with maximum width below whorl middle. Area between lowest strong spiral and lower suture remaining slightly concave. Sutures moderately incised. Lateral aspect of growth line trace prosocline, with weak upper and lower inflection points. Antispiral and basal sinuses shallow.

Measurements.—See Table 21.

Stratigraphic and Geographic Distribution.—AL: Lisbon Formation; GA, SC: McBean Formation[5], Lisbon Formation; TX, MS: Cook Mountain Formation; middle—upper Claibornian Stage, Middle Eocene.

Type Locality.—approx. 1.5 km south of Lisbon Landing, Alabama River, Monroe County, Alabama (AL-MO-4d).

Other Localities.—AL-CL-14(MCZ), AL-CL-16 (B), AL-CN-1 (B), AL-MO-1b (MCZ), MS-CL-1 (B), MS-CL-2 (B), MS-CL-7 (B), MS-CL-16 (B), MS-CL-17 (B), MS-CL-18 (B), MS-CL-19 (B), MS-NE-1 (B), MS-NE-10 (B), SC-AI-1 (B), SC-LE-1 (B), SC-LE-2 (B), SC-OR-5 (B), SC-OR-6 (B), SC-OR-7 (B), SC-OR-10 (B), SC-OR-11 (B), GA-BU-3 (B), GA-BU-7 (B).

Type Material.—holotype of *T. lisbonensis* Bowles USNM 498009, paratype USNM 497952.

Remarks/Discussion.—As noted by Erickson (1982), Bowles states that *lisbonensis* is "confined to the Claiborne of the eastern Gulf region," but then gives several Texas localities for its occurrence, apparently referring to specimens referred to *Palmerella dutexata* (Harris). This confusion highlights the similarity of *lisbonensis* to *P. femina* (Stenzel) and *P. dutexata* (Harris) which, as discussed above (p.57), are probably themselves ends of an intergrading series. *Palmerella lisbonensis* shares with these forms the prominence of a pair of carinae on the lower portion of early as well as late whorls, but it is distinct in attaining a greater size and much more elongate overall shape. In early whorls it shows a relatively high apical angle, similar to *femina,* but soon changes to a more columnar, cylindrical form.

On the basis of these morphological and stratigraphic relationships, it seems reasonable to suggest that *P. dutexata* (Harris) of the Cook Mountain, Upper Lisbon and Gosport Formations is a direct phyletic descendant of *P. femina* (Stenzel) from the Weches Formation, and that *P. lisbonensis* is a product of a cladogenetic event from this lineage, probably during deposition of the Cook Mountain/Upper Lisbon formations. As mentioned above, *lisbonensis* may have been close to the ancestry of *P. apita* (de Gregorio) from the Gosport and *P. arenicola* (Conrad) from the Moodys Branch.

Palmerella mortoni mortoni
(Conrad, 1830)
Plate 1, Figures 4–6,
Plate 2, Figures 6–8

Turritella mortoni Conrad, 1830, p.213–215, 221, pl.10, f.2; 1834, p.4 in part; 1835a, p.40 in part, not pl.15, f.11 [= *Haustator carinata* (I.Lea)]; 1846, p.219; 1865a, p.32; 1866, p.11; Tuomey, 1858, p.267, not p.270–272; not Aldrich, 1886a, p.9,13,46,55,58–60 [= *Palmerella mortoni postmortoni* Harris]; not Smith and Johnson, 1887, p.59 in part [= *Palmerella alabamiensis* Whitfield]; de Gregorio, 1890, p.122 in part, pl.11, f.7, copy Conrad, 1830, not pl.11, f.3–6,9 [= *Haustator carinata* (I.Lea)]; Cossmann, 1893, p.29; Harris, 1894a, p.302–304, f.3; 1896, p.110; not 1899a, p.74, pl.10, f.3,4 [= *P. m. postmortoni*]; not 1899b, p.299,308, pl.52, f.9 [=*Turritella* sp., *fide* Palmer and Brann, 1966, p.994], pl.55, f.4 [= *P. m. postmortoni*]; Clark, 1895, p.4; 1896, p.69, pl.13, f.1a-e; Clark and Martin, 1901, p.147, pl.26, f.1–4; not Veatch, 1906, pl.14, f.5,5a [= *P. m. postmortoni*]; Clark and Miller, 1912, p.92–100, 102,119,120; Guillaume, 1924, p.289,290; 1926, p.426; not Cooke, 1926, p.259,261,264, pl.94, f.2; not Semmes, 1929, f.59–2 [= *P. m. postmortoni*]; Palmer, 1937, p.195, pl.23, f.6,11, pl.24, f.14 [not 13 as in text]; Bowles, 1939, p.293, pl.33, f.14; Stenzel and Turner, 1942, card 83; Shimer and Shrock, 1944, p.493, pl.201, f.14–17, copy Clark and Martin, 1901; Brann and Kent, 1960, p.927 in part, nos. 2880,2883;2892,3904 only, *fide* Palmer and Brann, 1966, p.995; Vokes, 1961, p.49, pl.10, f.1; Palmer and Brann, 1966, p.994–5.

Turritella mortoni mediavia Bowles, 1939 in part, p.294, pl.33, f.3; not f.5.

Description.—Shell large to very large, of 20 to 25 whorls. Maximum observed whorl diameter 40 mm. Apical angle 22°; apical and pleural angles approximately equal. Sutures moderately deeply incised. Protoconch erect, homeostrophic, turbinate, of approximately 1.7–2.0 smooth, rounded whorls; P1 small.

[5] See Footnote 3, p.46.

Apical sculpture formula C_1 B_1 A_2. Primary spirals C and B appearing approximately simultaneously as broad, slightly angular prominence just below middle of whorl, and quickly diverging and becoming more acute, B becoming stronger than C. Primary A appearing within 0.5–0.75 whorl, remaining weaker than C for one to two whorls after which it is of approximately equal strength. Secondaries and finer spirals beginning at about whorls 8–10. Primary B and one or more secondaries remaining prominent on upper slope of carina, but more adapical spirals becoming obsolete. Whorl profile changing shortly after appearance of numerous secondary spirals, from medially to basally carinate, C becoming relatively more prominent and lower ¼ of whorl expanding outward. Area between C spiral and suture expanding and changing from relatively straight-sided to variably convex in profile. Whorl profile above carina becoming increasingly concave. Lateral aspect of growth line trace prosocline, with pronounced upper and lower inflection points and relatively deep sinus whose apex just above whorl middle. Lower inflection point usually high on lower part of whorl, causing spiral sinus to be relatively narrow and basal sinus relatively wide although both moderately deep.

Measurements.—See Table 22.

Stratigraphic and Geographic Distribution.—MD, VA: Aquia Formation (Piscataway and Paspotanza Members); SC: Black Mingo Group, Williamsburg Formation; Upper Paleocene.

Type Locality.—probably Piscataway Creek, Prince Georges County, Maryland (MD-PG-5).

Other Localities.—MD-AA-5 (B), MD-CH-7 (B), MD-PG-3(B), MD-PG-10 (B), VA-ST-4 (B), VA-ST-5 (B), VA-ST-6 (B), VA-ST-7 (B), VA-HA-2 (MCZ), SC-SU-2 (B), SC-BE-3 (VC), SC-CL-2 (B).

Type Material.—holotype? and 2 paratypes of *T. mortoni* Conrad ANSP 15508.

Remarks/Discussion.—"*Turritella mortoni* Conrad" and its close relatives are of special importance in both the evolutionary history of their clade in the Coastal Plain Paleogene, and the history of its study over more than a century and a half. *Turritella mortoni* was one of the first species to be described from the "Eocene" of North America (Conrad, 1830), and since that time it has been a commonly used index fossils (*e.g.*, Shimer and Shrock, 1944; Toulmin, 1977), and is one of the most characteristic and widely recognized macrofossil taxa of the lower Tertiary. The systematic status of "*T. mortoni*", however, has remained poorly understood. Many of the numerous references to it in the literature, as Bowles (1939) has noted, refer to other species, and the name "*T. mortoni*" has commonly been used "more in the sense of the group of basally carinate Paleocene and Lower Eocene turritellas than as a distinct specific entity" (1939, p. 293).

Four very similar named forms comprise what can be called "*Turritella mortoni* sensu lato." These are *T. mortoni* s.s. Conrad, 1830 from the Sabinian-aged Aquia Formation of Maryland and Virginia and Sabinian-aged Williamsburg Formation (Black Mingo Group) of South Carolina; *T. postmortoni* Harris, 1894a from the Sabinian-aged Nanafalia and Tuscahoma Formations (Wilcox Group) of the Gulf Coastal Plain; *T. mediavia* Bowles, 1939 from the Midwayan-aged Clayton Formation of the Gulf Coastal Plain; and *T.* "*premortoni*" (Govoni, 1983; Govoni and Hansen, in press) from the Midwayan-aged Brightseat Formation of Maryland. (As discussed above, *T. hilli* Gardner from the Midwayan-aged Kincaid Formation of Texas may be very close to *T.* "*premortoni*" and may represent a fifth member of this group.) (See Text-figure 15 for stratigraphic relationships.) All four of these taxa share the following features: 1) a moderate and rounded to pronounced and sharp-edged carina, in which the C spiral is most prominent, 2) moderate apical angles, approximately equal to pleural angles, 3) medium to large size.

Morphologic relationships among these forms have usually been approached only in very general and qualitative terms. Clark and Martin (1901, p.147) note that "*T. mortoni*" from Maryland and Virginia "shows very great variation in the form and decoration of the whorls, and if it were not for the great number of intermediate types one might readily establish several independent species." Andrews (1971, 1974) has attempted a preliminary morphometric analysis of this variation, but uses only 37 specimens and does not make reference to taxa from elsewhere on the Coastal Plain. He is thus unable to draw any systematic conclusions.

I have attempted to resolve the morphological relationships among at least some of these forms by multivariate morphometric analysis. Details of the methods and specimens used are presented in Appendix 1.

Table 22.—Measurements of *Palmerella mortoni mortoni* (Conrad). Abbreviations as in Table 10.

	MD	*MH*	*WN*
ANSP 15508 holotype ?	23.5	59.9	9.5
ANSP 15508 paratype	22.7	50.6	8.5
USNM 497990	26.5	98.0	14.0
MCZIP 29307	31.0	110.0	11.5
MCZIP 29099	37.9	104.5	9.5

Table 23.—Results of factor analysis of specimens of the Recent species *Turritella terebra* (Linnaeus). Variance explained by first five factor axes.

Factor	*cumulative proportion of variance*
1	0.4018
2	0.5645
3	0.6396
4	0.7077
5	0.7553

For *mortoni* and its close allies, I have subjected large samples of specimens from Virginia and Maryland (*mortoni* s.s.) and Alabama (usually assigned to *post-mortoni* Harris) to factor analysis. These results can be compared to a similar analysis of a Recent species, the type species of the genus *Turritella* Lamarck, *Turritella terebra* (Linné).

Text-figure 17 shows the results for *T. terebra*. A total of 78 variables on each of 86 specimens were analyzed. The first three factors together explain almost 64% of the total variance (Table 23). In the factor

Table 24.—Results of factor analysis of specimens of the Recent species *Turritella terebra* (Linnaeus). Rotated factor loadings of each variable on each of the first three factor axes. Variables as indicated in Text-figure 3.

Variable	*factor 1*	*factor 2*	*factor 3*	Variable	*factor 1*	*factor 2*	*factor 3*
WH1	−0.438	0.143	−0.090	WW11	0.419	0.125	0.462
SW1	−0.440	0.142	−0.108	IN11	0.275	0.032	0.448
WW1	−0.439	0.142	−0.108	WH12	0.668	0.083	0.252
IN1	−0.439	0.141	−0.113	SW12	0.692	0.058	0.250
WH2	−0.649	0.057	−0.060	WW12	0.704	0.103	0.212
SW2	−0.646	0.059	−0.042	IN12	0.499	0.084	0.205
WW2	−0.650	0.059	−0.049	WH13	0.782	0.246	0.009
IN2	−0.639	0.049	−0.051	SW13	0.786	0.210	0.016
WH3	−0.818	−0.099	0.128	WW13	0.786	0.241	0.011
SW3	−0.810	−0.095	0.138	IN13	0.721	0.249	0.023
WW3	−0.806	−0.101	0.120	WH14	0.829	0.327	−0.143
IN3	−0.783	−0.096	0.126	SW14	0.828	0.297	−0.135
WH4	−0.830	−0.270	0.196	WW14	0.829	0.326	−0.129
SW4	−0.818	−0.261	0.220	IN14	0.822	0.340	−0.111
WW4	−0.806	−0.268	0.194	WH15	0.795	0.393	−0.195
IN4	−0.746	−0.189	0.242	SW15	0.796	0.363	−0.185
WH5	−0.607	−0.514	0.363	WW15	0.795	0.388	−0.185
SW5	−0.540	−0.520	0.367	IN15	0.780	0.404	−0.163
WW5	−0.530	−0.521	0.338	WH16	0.716	0.463	−0.272
IN5	−0.538	−0.400	0.352	SW16	0.722	0.432	−0.262
WH6	−0.298	−0.613	0.564	WW16	0.722	0.453	−0.263
SW6	−0.190	−0.612	0.577	IN16	0.617	0.429	−0.229
WW6	−0.173	−0.611	0.519	WH17	0.479	0.612	−0.354
IN6	−0.261	−0.452	0.510	SW17	0.482	0.584	−0.376
WH7	−0.223	−0.650	0.590	WW17	0.483	0.600	−0.363
SW7	−0.156	−0.634	0.603	IN17	0.427	0.660	−0.345
WW7	−0.079	−0.621	0.495	WH18	0.249	0.714	−0.430
IN7	−0.192	−0.314	0.496	SW18	0.253	0.685	−0.451
WH8	−0.160	−0.296	0.863	WW18	0.249	0.717	−0.429
SW8	−0.070	−0.269	0.873	IN18	0.217	0.794	−0.325
WW8	−0.009	−0.260	0.761	WH19	0.073	0.869	−0.007
IN8	−0.164	−0.155	0.607	SW19	0.077	0.852	−0.016
WH9	−0.012	−0.221	0.876	WW19	0.074	0.868	−0.003
SW9	0.052	−0.197	0.884	IN19	0.066	0.894	0.042
WW9	0.133	−0.145	0.737	WH20	0.015	0.807	0.138
IN9	−0.075	−0.043	0.578	SW20	0.015	0.807	0.137
WH10	0.032	−0.065	0.911	WW20	0.016	0.808	0.140
SW10	0.074	−0.053	0.916	WH			
WW10	0.158	−0.014	0.767	SW			
IN10	−0.058	0.044	0.571	WW			
WH11	−0.103	0.116	0.252	IN			
SW11	0.346	0.094	0.619				

1—factor 2 plot (Text-fig. 17A), most (84%) of the specimens analyzed cluster around the factor 1 axis. The 14 specimens that do not do so fall along a negatively sloping line in the first quadrant, scoring high on factor 2. Ten of these 14 specimens also fall away from the rest in the factor 2—factor 3 plot (Text-fig. 17B), scoring negatively on factor 3. The loadings in the varimax-rotated factor matrix (Table 24) suggest that these 14 specimens differ primarily in the later whorls (17–20).

These 14 specimens are not randomly drawn from all samples analyzed; 11 of the 14 come from two specimen lots from the Philippines (TEREBR1, TEREBR18; Appendix 1), suggesting the possibility that the variability noted here may represent differentiation at the population level. This possibility is supported by the distribution of *T. terebra* in the western Pacific. It is found today in considerable numbers in Taiwan (Kuroda, 1941), the south-central coast of the Chinese mainland (Chin, 1941; Chung, 1981), Hong Kong (Wu and Richards, 1981), the Philippines (Faustino, 1928), New Guinea (Hinton, 1972), Java (Roberts *et al.*, 1982) and northern Australia (Garrard, 1972; Wilson, 1993). This range is larger than that of most Recent turritellid species, raising the possibility that *T. terebra* may include a number of diverging populations.

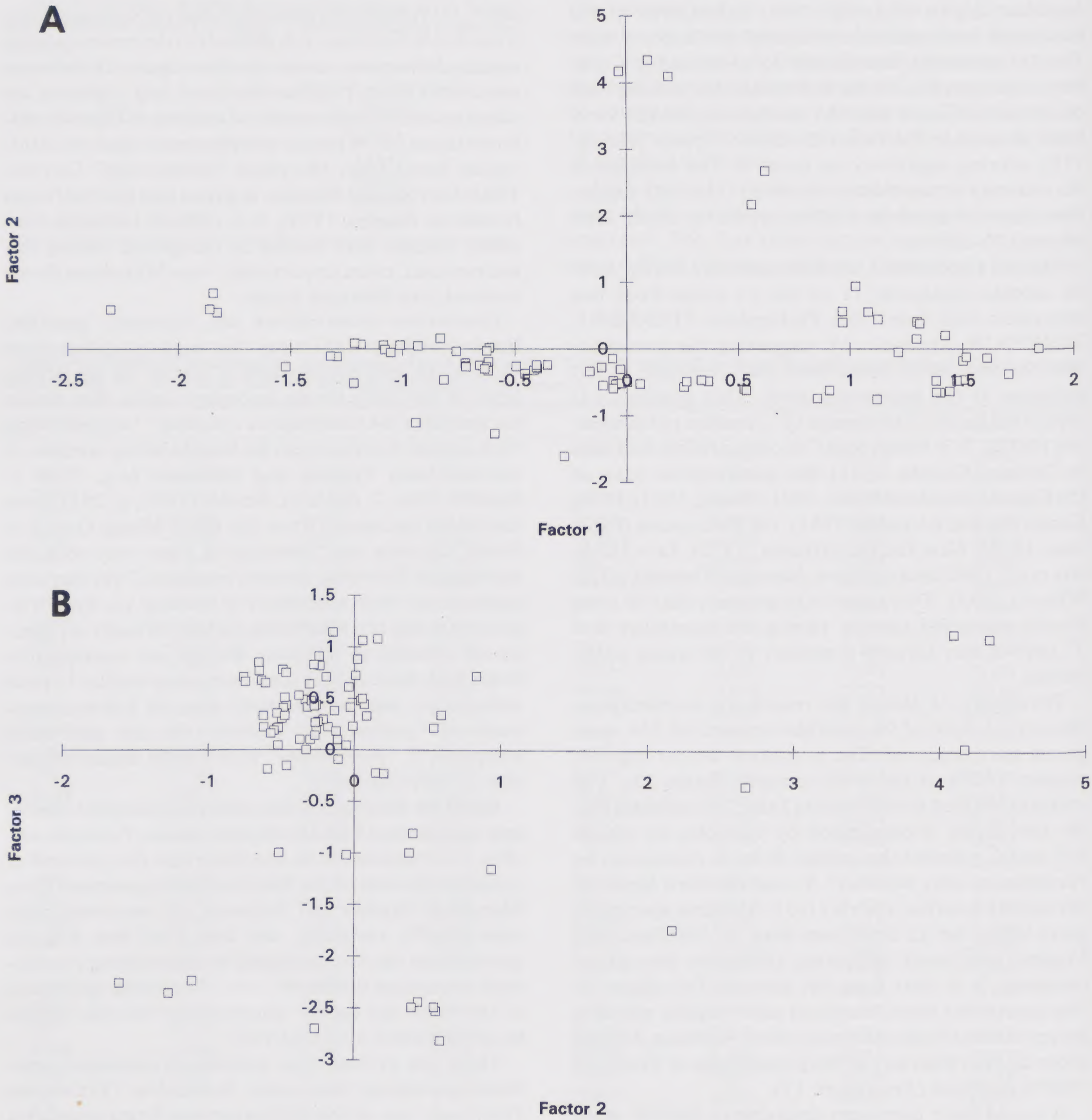
Text-figure 18 shows the results for *mortoni/postmortoni*. A total of 90 variables on each of 354 specimens were analyzed. The first three factors together explain 57.2% of the total variance (Table 25). The varimax-rotated factor matrix (Table 26) indicates that the first factor is dominated by variables on whorls 4,5, and 6, whereas the second factor is dominated by variables on later whorls (7–9) and the third factor by variables on earlier whorls (1–3). Alabama specimens score higher on all three axes than do Maryland and Virginia specimens, indicating differences throughout ontogeny. It is clear from the plots in Text-figure 18 that specimens from Maryland and Virginia are, as a group, distinct from specimens from Alabama, but not more distinct than any of the populations of *Turritella terebra* analyzed (Text-figure 17).

It would have been very desirable to include other forms and samples in this analysis, especially specimens assigned to *mortoni* from the Sabinian-aged Black Mingo Group of South Carolina (*e.g.,* Van Nieuwenhuise and Colquhoun, 1982), as well as specimens of *T. mediavia* Bowles, 1939 and *T.* "*premortoni*" Govoni, 1983, but too few well-preserved specimens of any of these were available for quantitative analysis. These limitations of material produce substantial limitations of interpretation in attempts at a comprehensive understanding of evolution within "*mortoni* sensu lato": 1) Without morphometric data on Sabinian forms from South Carolina, it is difficult to determine whether the differences shown in Text-figure 18 between specimens from Virginia-Maryland and Alabama are clinal or more characteristic of discrete subspecific differentiation. 2) Without morphometric data on Midwayan forms from Maryland ("*premortoni*" Govoni, 1983; Govoni and Hansen, in press) and the Gulf coast (*mediavia* Bowles, 1939), it is difficult to decide how many discrete taxa should be recognized during this interval and, more importantly, how Midwayan forms evolved into Sabinian forms.

Qualitative observations are, however, possible. Bowles (1939, p. 295) states that *mediavia* differs from *mortoni* s.s. and *postmortoni* of Harris "in the persistence of the fairly strong secondary carina that makes the profile of the whorls more rounded," but specimens with similar sculpture can be found among samples of *mortoni* from Virginia and Maryland (*e.g.,* Plate 1, figure 4, Plate 2, figure 6). Bowles (1939, p. 295) notes that some specimens from the Black Mingo Group of South Carolina are "identical in every way with the holotype of *Turritella mortoni mediavia,*" yet they also agree closely with specimens of *mortoni* s.s. from Virginia. Among the Midwayan forms, virtually all specimens referred to *mediavia* Bowles are considerably larger and more robust (and thus more similar to both *mortoni* s.s. and *postmortoni*) than all known specimens of "*premortoni*" Govoni. (In size and adult sculpture, *T.* "*premortoni*" in fact most closely resembles *T. hilli* Gardner.)

Based on the multivariate analysis presented above, and comparison with the Recent species *Turritella terebra,* it is reasonable to conclude that the patterns of variation showed by the Sabinian-aged specimens from Maryland-Virginia and Alabama are consistent with intra-specific variation, and that Gulf and Atlantic populations can be considered as representing two distinct subspecies within *mortoni.* Carolinian specimens of the same age appear intermediate but this cannot be documented quantitatively.

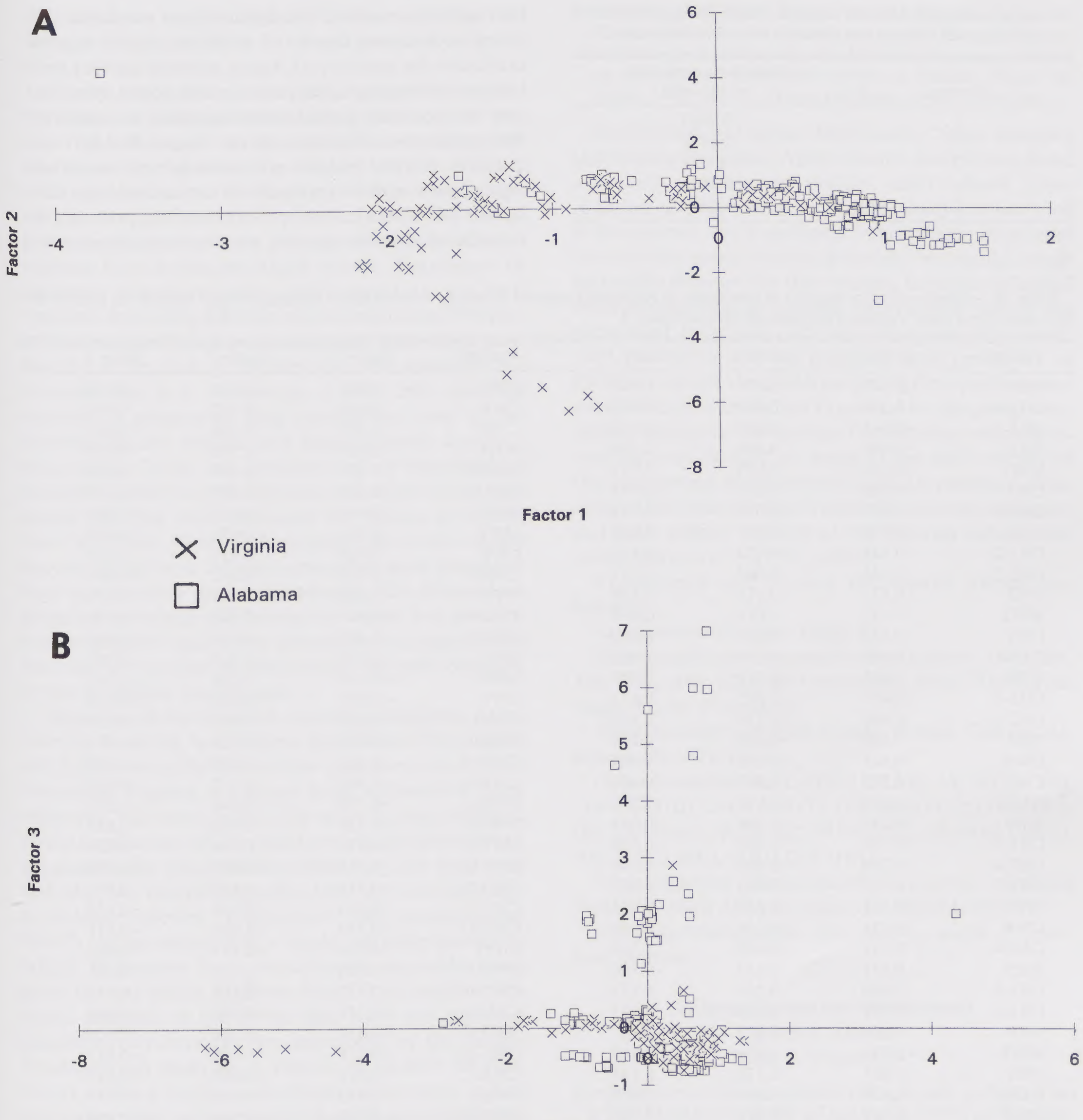
There are at least four possible evolutionary relationships among these taxa. In the first (Text-figure 19A), only one of the Midwayan-age forms (*mediavia* or "*premortoni*") is ancestral to both *postmortoni* and *mortoni* s.s. In favor of "*premortoni*" being this single ancestral form is the close similarity of its protoconch and early teleoconch whorls to those of *mortoni* s.s. (Govoni, 1983, p. 103; see Plate 1, figs. 2,6). In favor of *mediavia* as representative of this single ancestral form is the greater (albeit qualitative) similarity in adult size and sculpture of the Sabinian forms to *mediavia* than to "*premortoni*". Against this interpretation is the lack of apparent *mediavia* descendants where they might



Text-figure 17.—Results of factor analysis of specimens of *Turritella terebra*. **A**. first and second factor axes. **B**. Second and third factor axes. See Appendix 1 for specimens used and details of analysis.

be expected if *mediavia* was directly ancestral to *postmortoni* (*i.e.*, in post-Clayton fossiliferous sediments of the Gulf coast, such as the Matthews Landing Member of the Porters Creek Formation, and the Naheola Formation).

The second scenario (Text-figure 19B) suggests that Atlantic and Gulf Coastal Plain lineages evolved more or less separately during the Paleocene; "*premortoni*" is ancestral to *mortoni* s.s., and *mediavia* to *postmortoni*. Such separation is supported by the differences within both Midwayan and Sabinian forms. Taken as a whole, *mortoni* s.s. from the Aquia of Maryland and



Text-figure 18.—Results of factor analysis of specimens of *Palmerella mortoni sensu lato*. **A**. first and second factor axes. **B**. Second and third factor axes. × represents specimens from Virginia (*mortoni* s.s.); □ represents specimens from Alabama (usually referred to *postmortoni* Harris). See Appendix 1 for specimens used and details of analysis.

Virginia shows differences in the ontogenetic development of the basal carina compared to *postmortoni* from the Alabama Wilcox. The expansion of the carina is allometric in both forms, but in *postmortoni* this expansion stops before largest size is reached, whereas in *mortoni* s.s. it continues throughout growth; the greater degree of carination in *postmortoni* is a result of a higher allometric scaling exponent (Allmon, 1994).

Table 25.—Results of factor analysis of specimens of *Palmerella mortoni* (Conrad). Variance explained by first five factor axes.

Factor	*cumulative proportion of variance*
1	0.3505
2	0.4828
3	0.5720
4	0.6376
5	0.6953

Govoni's "*premortoni*" is distinct from *mediavia,* differing in size and degree of sculpture, but is a good candidate for ancestry of Aquia *mortoni* s.s. not only because of its geographic position and apical form, but also its moderate, rounded carina which is similar to that of the lowest *mortoni* in the Aquia. Bowles' *mediavia* is similar to both *postmortoni* and some late Aquia *mortoni* in its pronounced carina and large size. Under this scenario the four forms should probably be considered separate species, since temporally coexist-

Table 26.—Results of factor analysis of specimens of *Palmerella mortoni* (Conrad). Rotated factor loadings of each variable on each of the first three factor axes. Variables as indicated in Text-figure 3.

Variable	*factor 1*	*factor 2*	*factor 3*	Variable	*factor 1*	*factor 2*	*factor 3*
WH1	−0.047	0.064	0.747	MW7	0.602	0.574	0.054
CH1-1	−0.048	0.068	0.740	CW7	0.643	0.552	0.070
CH2-1	−0.044	0.055	0.742	CAN7	0.567	0.546	−0.003
SW1	−0.046	0.060	0.744	WH8	−0.130	0.346	0.111
MW1	−0.046	0.059	0.749	CH1-8	0.251	0.699	0.002
CW1	−0.046	0.061	0.751	CH2-8	0.400	0.482	0.107
CAN1	−0.042	0.057	0.744	SW8	0.433	0.612	−0.014
WH2	0.132	0.017	0.840	MW8	0.459	0.633	0.020
CH1-2	0.125	0.022	0.851	CW8	0.539	0.631	0.054
CH2-2	0.144	0.002	0.769	CAN8	0.331	0.632	−0.047
SW2	0.127	0.018	0.829	WH9	−0.248	0.372	0.071
MW2	0.132	0.016	0.846	CH1-9	−0.341	0.542	−0.118
CW2	0.135	0.015	0.840	CH2-9	0.053	0.523	−0.044
CAN2	0.140	0.010	0.832	SW9	−0.147	0.504	−0.160
WH3	0.463	−0.058	0.622	MW9	−0.153	0.538	−0.142
CH1-3	0.497	−0.095	0.613	CW9	−0.072	0.543	−0.123
CH2-3	0.493	−0.110	0.561	CAN9	−0.207	0.447	−0.155
SW3	0.489	−0.094	0.609	WH10	−0.503	0.229	0.057
MW3	0.501	−0.096	0.604	CH1-10	−0.803	0.060	−0.053
CW3	0.502	−0.097	0.604	CH2-10	−0.647	0.177	−0.021
CAN3	0.516	−0.111	0.568	SW10	−0.739	0.044	−0.062
WH4	0.743	−0.046	0.334	MW10	−0.758	0.056	−0.059
CH1-4	0.732	−0.039	0.329	CW10	−0.737	0.068	−0.053
CH2-4	0.708	−0.062	0.318	CAN10	−0.765	0.007	−0.076
SW4	0.722	−0.033	0.343	WH11	−0.576	0.107	0.067
MW4	0.737	−0.036	0.344	CH1-11	−0.804	−0.161	−0.030
CW4	0.734	−0.034	0.344	CH2-11	−0.739	−0.015	−0.011
CAN4	0.741	−0.043	0.314	SW11	−0.765	−0.191	−0.044
WH5	0.841	0.157	0.146	MW11	−0.783	−0.167	−0.036
CH1-5	0.820	0.163	0.137	CW11	−0.772	−0.164	−0.037
CH2-5	0.793	0.118	0.151	CAN11	−0.776	−0.202	−0.048
SW5	0.802	0.179	0.127	WH12	−0.230	0.203	0.106
MW5	0.830	0.176	0.119	CH1-12	−0.578	−0.500	−0.013
CW5	0.827	0.178	0.134	CH2-12	−0.561	−0.480	−0.012
CAN5	0.836	0.161	0.097	SW12	−0.573	−0.508	−0.014
WH6	0.767	0.352	0.064	MW12	−0.573	−0.504	−0.014
CH1-6	0.714	0.393	0.088	CW12	−0.573	−0.514	−0.014
CH2-6	0.609	0.363	0.074	CAN12	−0.575	−0.487	−0.015
SW6	0.714	0.378	0.049	WH13	−0.133	−0.726	−0.047
MW6	0.736	0.397	0.054	CH1-13	−0.133	−0.721	−0.047
CW6	0.754	0.388	0.086	CH2-13	−0.130	−0.720	−0.047
CAN6	0.746	0.358	0.014	SW13	−0.134	−0.713	−0.047
WH7	−0.090	0.327	0.116	MW13	−0.133	−0.715	−0.047
CH1-7	0.534	0.599	0.036	CW13	−0.133	−0.712	−0.047
CH2-7	0.492	0.438	0.154	CAN13	−0.132	−0.724	−0.047
SW7	0.563	0.553	0.030				

ing forms are morphologically distinct and the two lineages are presumed to have evolved independently over geological time.

Finally, Midwayan forms may represents a single, variable and geographically widespread species that evolved, in toto, into another variable and widespread species in the Sabinian (Text-figure 19C). In support of this hypothesis is the highly variable morphology within *mortoni* from the Aquia. Andrews (1971) suggests that a less carinate form evolved into a more carinate form within the Aquia section. Text-figure 18 indicates that *postmortoni* and *mortoni* s.s. are both variable, but along different multivariate axes. Whether "*premortoni*" and *mediavia* could have been conspecific is not clear, given their size and sculpture differences, but it is interesting to note that *mediavia* occupies a geographic area in-between those of the morphologically similar and approximately synchronous *hilli* in Texas and "*premortoni*" in Maryland. A possible variant on this scenario is similar to one suggested that has been discussed for human evolution (see Van Valen, 1966). Different populations of a single species could have crossed a morphological threshold to a new morphology independently. The descendant populations would still belong to a single and more or less genetically continuous species, but its populations had not all evolved simultaneously or with constant levels of genetic interchange.

Based on all information currently available, I tentatively favor the last of these hypotheses (Text-figure 19C). Data are sufficient to show that *mortoni* s.s. from Maryland-Virginia is distinct from *postmortoni* from Alabama, but not substantially more so than different living populations of *Turritella terebra*; specimens from geographically intermediate areas may (or may not) link the two morphologically. Data are not sufficient to indicate whether "*premortoni*" and *mediavia* (and *hilli* ?) can be united into a single, variable species or which Midwayan form most closely resembles (and gave rise to) which Sabinian form. It is possible that larger samples of the forms that were not analyzed quantitatively here can be assembled in the future. Pending such analyses, I choose to include all four forms within a single, variable species *mortoni,* and to recognize them as geographic/chronologic subspecies.

Palmerella mortoni mediavia (Bowles, 1939)
Plate 2, Figures 1,9

? *Turritella mortoni* Conrad var. Harris, 1894b, p.48, pl.3, f.5; Brann and Kent, 1960, p.928. *Turritella mortoni* Conrad ? Harris, 1894b, p.47,48; 1896, p.16,17; McCallie, 1908, p.335 [not p.235 as in Bowles, 1939]; Veatch and Stephenson, 1911, p.219,220; Stephenson and Veatch, 1915, p.69; Stephenson and Crider, 1916, p.48, 49, 51–53; Brantly, 1920, p.144,146 [only]; Cooke, 1936, p.50; not Conrad, 1830; Toulmin, 1977, pl. 8, f.8.

? *Turritella saffordi* Gabb. Harris, 1896, p.110, in part, pl.11, f.8, [*T.mortoni* var. on plate caption]; not Gabb, 1860, p.392.

Turritella mortoni mediavia Bowles, 1939, p.294 in part, pl.33, f.5; not pl.33, f.3 [= ? *Palmerella mortoni* s.s. Conrad]; Stenzel and Turner, 1942, card 79; Palmer and Brann, 1966, p.995–996.

Description.—Original description: "Spire abruptly tapering for the genus. Apical whorls sharply angulated anteriorly, concave in profile; adult whorls more rounded, almost convex in profile, sharply constricted at the sutures, which are linear but distinctly impressed between the apical whorls, gradually becoming deeper and wider between the later whorls. Sculpture of apical whorls consisting of a strong basal carina with a less prominent revolving cord near the posterior suture; both the carina and the posterior cord persistent on the adult whorls, the posterior giving the whorls a more rounded appearance than is general in the group. Secondary sculpture consisting of numerous very fine revolving lines, beaded on some of the early whorls by the intersection of the growth lines. Incremental striae distinct and sharply flexed medially, curving out again and then slightly reflexed at the anterior suture. Aperture unknown." (1939, p.294)

Protoconch and earliest teleoconch whorls unknown.

Measurements.—See Table 27.

Stratigraphic and Geographic Distribution.—AL, GA, MS, TN, AR: Clayton Formation; lower Midwayan Stage, Lower Paleocene.

Type Locality.—Prairie Creek, Wilcox County, Alabama (AL-WI-9).

Other Localities.—AL-HE-2 (TLM), AL-HE-3 (VS), GA-CL-3 (B), GA-CL-6 (T), GA-SL-3 (VS), GA-MA-1 (B), TN-HA-12 (US), AR-PU-4 (SC), AR-WH-1 (HA), AR-WH-2 (SC), AR-LO-1 (HA).

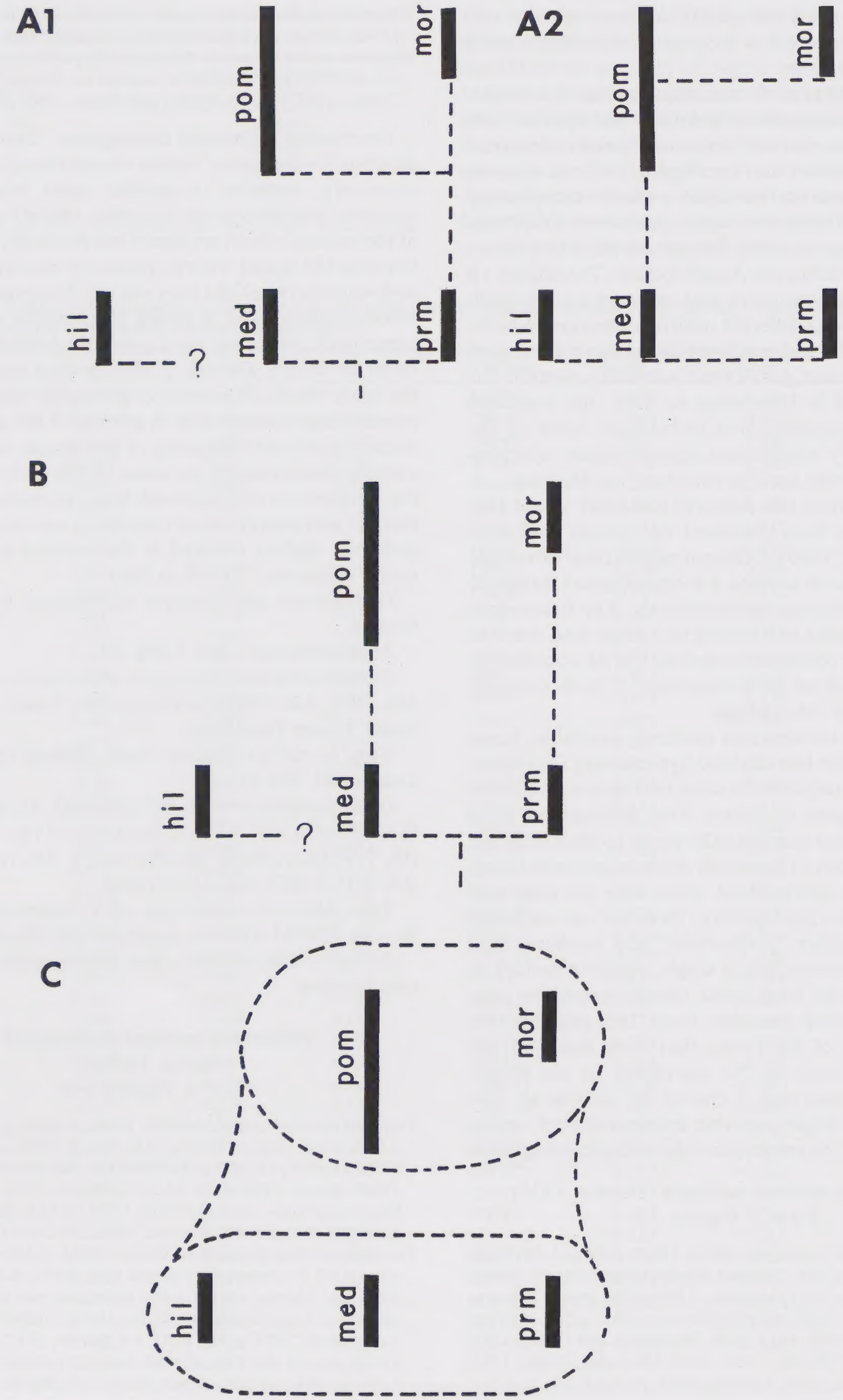
Type Material.—holotype of *T. mortoni mediavia* Bowles USNM 495146, paratype USNM 495147.

Remarks/Discusssion.—See above, under *P. mortoni mortoni.*

Palmerella mortoni postmortoni
(Harris, 1894a)
Plate 2, Figures 2–5

Turritella mortoni Conrad. Aldrich, 1886a, in part, p.13,55,58; not p.9,46,59,60; Harris, 1899a, p.74,pl.10, f.4; 1899b, p.308, in part, pl.55, f.4, not pl.52, f.9 [=*Turritella* sp., *fide* Palmer and Brann, 1966]; Veatch, 1906, pl.14, f.5,5a; Guillaume,1924, p.289 in part [not Claiborne as indicated]; 1926, p.425; Cooke, 1926, p.259,261,264, pl.94,f.2; Semmes, 1929, f.59–2; not Conrad, 1830.

Turritella mortoni postmortoni Harris, 1894a, p.302–304, in part, f.1, not f.2 [= *Palmerella mortoni* s.s.]; 1899a, p.75, pl.10, f.3; Clark and Martin, 1901, p.147–148 in part, not pl.26, f.5 [=*P. mortoni* s.s.]; not Grabau and Shimer, 1909, f.1064d [= *P.mortoni* s.s.]; Bowles, 1939, p.298, pl.33, f.4; Palmer, 1937, p.188, pl.23, f.8–10; Stenzel and Turner, 1942, card 95; LeBlanc *in* Barry and LeBlanc, 1942, pl.104, in part, pl.13, f.11; Shimer and Shrock,


A1
pom
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B
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Table 27.—Measurements of *Palmerella mortoni mediavia* (Bowles). Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 495146 holotype	19.0	41.0	7.5

Table 28.—Measurements of *Palmerella mortoni postmortoni* (Harris). Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 497992 hypotype	23.0	65.0	10.5
MCZIP 29308	26.6	74.3	10.5

1944, p.498 in part, not pl.201, f.17 [=*P. mortoni* s.s.]; Brann and Kent, 1960, p.928, in part, not No. 3903 [= *P. mortoni* s.s.]; Palmer and Brann, 1966, p.996; Toulmin, 1977, p.232, pl.29, f.9.

Turritella humerosa Conrad. Trowbridge, 1932, pl.31, f.6,7, copies Veatch, 1906, after Harris, 1899a [PRI 270, 271, not USNM 11754 as in Trowbridge]; not Conrad, 1835b.

Turritella postmortoni Harris. Toulmin, 1969, pl. 1, f.14.

Turritella sp. Toulmin, 1977, pl.29, f.12,13.

Description.—Shell large, of 15 to 20 whorls. Maximum observed whorl diameter 27.0 mm. Apical angle varies from 19°; apical and pleural angles approximately equal. Protoconch and earliest teleoconch whorls unknown. Sutures not deeply incised. Spiral sculpture on earliest whorls observed (dia. = 0.75 mm) consisting of three moderately prominent spirals, one in middle of whorl and one close to each suture, middle spiral being strongest. In succeeding whorls, upper and lower spirals moving toward center, space between upper and middle spirals becoming greater than that between lower and middle. Within four to five whorls, secondary spirals appearing between upper and middle primaries, between upper primary and suture, and immediately associated with lower suture. Further intercalaries continuing to appear on succeeding whorls. Teleoconch whorls wider than high. Profile of earliest known whorls generally straight-sided, angulated in middle by prominent middle primary spiral. On succeeding whorls, lower primary spiral surpassing middle spiral in strength; whorl profile becoming basally carinate; area between lower primary spiral and spiral at suture becoming slightly concave in profile. This area remaining approximately same size on succeeding whorls, while area beneath lowest spiral expands, the point of contact of following whorl shifting relatively inward with carina coming to overhang suture with a surface originally roughly horizontal, becoming angled downward and slightly convex outward in profile with carina moving relatively upward on the whorl. On late whorls profile markedly concave above the carina and slightly convex below. Carina varying in profundity from acute angulation in lower half of whorl to flaring, adapically turned flange several mm wide, often undulating in its lateral trace. Outer edge of carina almost always made of single spiral rib, but single weaker spiral just below edge usually visible. Lateral aspect of growth line trace markedly prosocline, with well developed upper and lower inflection points and a moderately deep sinus, apex of which is just above whorl middle. Lower inflection point usually relatively high on lower ½ of whorl, causing spiral sinus to be relatively narrow and basal sinus to be relatively shallow.

Measurements.—See Table 28.

Stratigraphic and Geographic Distribution.—AL,GA: Nanafalia Formation (*Ostrea thirsae* beds, Grampian Hills Member), Tuscahoma Formation (Bells Landing Member, Greggs Landing Member); TX,LA: Pendleton Formation, Marthaville Formation; Sabinian Stage, Upper Paleocene.

Type Locality.—Bells Landing, Alabama River, Monroe County, Alabama (AL-MO-3)

Other Localities.—AL-WI-1 (B), AL-WI-18b (B), AL-WI-18c (C), AL-WI-55 (B), AL-WI-57 (T), AL-WI-58 (T), AL-MA-1 (B), AL-PI-1 (B), AL-PI-6 (T), AL-CH-6 (B), AL-CH-11 (T), AL-CH-12 (T), AL-DA-1 (MCZ), AL-DA-4 (T), AL-MO-5 (B), AL-HE-4 (T), TX-SA-5 (B), TX-SA-5C (L), TX-SA-19 (L), LA-NA-5 (L), LA-NA-12 (L), LA-NA-15 (L), LA-NA-16 (L), LA-NA-17 (L), LA-SA-20 (WW), LA-SA-21 (WW), LA-SA-22 (WW), GA-HE-1 (MCZ), GA-CL-2 (MCZ), GA-CL-7 (ANS).

Type Material.—lectotype of *T. mortoni postmortoni* Harris lost (*fide* Palmer and Brann, 1966, p.996), hypotype (Bowles, 1939) USNM 497992.

Remarks/Discussion.—Harris' *postmortoni* differs qualitatively from *mortoni* s.s. principally in being smaller, and in frequently showing a sharper and more pronounced basal carina, but overlaps considerably in

←

Text-figure 19.—Four possible evolutionary scenarios for the forms most closely related to *Palmerella mortoni* (Conrad). mor = *Palmerella mortoni* s.s., pom = *Palmerella mortoni postmortoni,* prm = *Palmerella mortoni* ssp. ("*premortoni*"), med = *Palmerella mortoni mediavia,* hil = *Palmerella hilli* Gardner. A1, A2. Only one phyletic link between Sabinian and Midwayan forms, either between the Gulf coast forms *mediavia* and *postmortoni,* or the Atlantic coast forms *mortoni* s.s. and "*premortoni.*" B. Atlantic and Gulf lineages are separate from each other throughout Midwayan and Sabinian times. C. Gulf and Atlantic forms continually interbreeding throughout Paleocene and earliest Eocene times, forming one broad and highly variable phyletic lineage. This is the hypothesis favored here.

general shell form. The results of the factor analysis (Text-figure 18) indicate that there are whorl shape differences between the Alabama and Virginia/Maryland specimens at all ontogenetic stages.

An interesting feature showed by several individuals of *postmortoni* is a doubling of the carina by the expansion of a secondary spiral just above the C spiral (see Plate 2, Figures 2,3,5). Toulmin (1977, pl.29, f.12,13) suggested that these forms represent a distinct species, but all intermediate conditions exist between a simple, single carina and a truly double carina of two equal-strength ribs. Most interesting is that some individuals of "*T.*" *praecincta* Conrad also show a double carina (Plate 14, Figure 3).

Palmerella mortoni, ssp.

Haustator premortoni Govoni, 1983, p. 104, pl.5, f.1–5.

Description.—Govoni (1983) provides the following description: "Shell medium-size, tapering, turriculate. Suture narrowly impressed. Protoconch erect, homeostrophic, turbinate, of about 3 smooth, rounded, rapidly expanding volutions; first volution minute, initially somewhat depressed; protoconch merges into teleoconch without percepible break. Whorls of teleoconch wider than high; total number of volutions unknown. Primary spiral threads B and C may appear on earliest juvenile whorl simultaneously (B_1 C_1) or, more frequently, C may appear just slightly ahead of B (B_2 C_1); within a single volution, primary spiral thread a appears just slightly posterior of the midpoint between B and the posterior suture, while at the same time B shifts slightly anteriorly of midwhorl and strengthens rapidly relative to c, forming a sharp, raised cord, and yielding the sculptural pattern which dominates the remaining juvenile whorls (a_3 B_2 c_1 d); primary spiral thread d seems to appear very early but remains more or less obscured beneath succeeding whorls. First fine secondary thread appears no later than fourth to fifth teleoconch whorl between primary spiral a and the posterior suture; additional secondary threads added progressively starting at sixth to seventh whorl, first between primaries a and B, then between B and c; a single secondary thread does not appear between c and anterior suture until eigth to ninth (early adolescent) volution, with 3 or 4 additional threads or weak cords not appearing in interspace until later adolescent to mature whorls. Starting in earlier adolescent whorls, many spirals, particularly stronger ones, may become finely but distinctly beaded where intersected by growth lines; beading persists throughout mature whorls but may become subdued, or late in ontogeny beads may merge and be incorporated into strong, elongate, wavey wrinkles as growth lines strengthen and become raised and crinkled. Whorl profile convex and submedially carinate in juvenile whorls; with addition and strengthening of secondary spirals in conjunction with relative weakening of primaries a and b, whorl sides of adolescent whorls initially flatten then quickly become shallowly concave medially above low, sharp, carinate basal angulation that overhangs succeeding whorl; basal angulation formed by relative strengthening of primary c and sometimes the secondary spiral below; in mature whorls basal carination becomes rounded and increases in prominence, whorl sides become somewhat more constricted medially, and posterior third of whorl may become broadly convex or develop a very low secondary carination at position of primary spiral a. Mature whorls covered by numerous fine spiral threads that tend to be of subequal strength on posterior third of whorl, of similar but more obviously alternating strength medially, and strongest on and below the basal carina; in latest whorls spirals appear wavey and disrupted by intersection of strongly wrinkled growth lines; flattened whorl base covered by numerous relatively coarse subequal spiral threads. Growth lines sinuous, indistinct at first, becoming increasingly prominent in mature whorls; on upper surface of mature whorls above basal carina, growth lines form a deep, nearly symmetrical spiral lateral sinus with gently curved and acutely inclined limbs, with vertex immediately above midwhorl and corresponding to point of maximum constriction of whorl side; lines recurve to form prospiral sinus of similar width and depth centered upon basal carina, then continue in broad antispiral arc across whorl base to columella. Aperture incompletely known, possibly subquadrate; parietal region calloused."

Measurements.—See Table 29.

Stratigraphic and Geographic Distribution.—MD: Brightseat Formation; Lower Paleocene.

Type Locality.—Southwest Branch, W of Capital Beltway, Prince Georges County, Maryland (MD-PG-12).

Other Localities: MD-PG-13 (GO), MD-PG-14 (GO).

Type Material: holotype and 75 paratypes of *Haustator "premortoni"* Govoni USNM

Remarks/Discusssion.—See above, under *P. mortoni mortoni* and Govoni and Hansen (in press).

Table 29.—Measurements of *Palmerella mortoni* ssp. ("*premortoni*" Govoni). Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM holotype	14.9	39.9	6.5
USNM paratype	4.8	13.1	8

Palmerella pleboides (Vaughan, 1895)
Plate 6, Figures 1–3

Turritella pleboides Vaughan, 1895, p.213, *nomen nudum*; Bowles, 1939, p.311, pl.33, f.7; Stenzel and Turner, 1942, card 92, f.4–6, copies Vaughan, 1895, f.7; Palmer and Brann, 1966, p.1001.
Mesalia pleboides Vaughan, 1896, p.36,44, pl.3, f.4–6; Schuchert, Dall, Stanton and Bassler, 1905, p.401; Palmer, 1937, p.208, pl.27, f.5,11,12; Brann and Kent, 1960, p.549,550.

Description.—Shell small, of 10 to 15 whorls. Maximum observed whorl diameter 7.0 mm. Apical angle 20°; pleural angle may be slightly less than apical angle. Sutures relatively deeply incised. Protoconch suberect, homeostrophic, turbinate, of 1.5–1.75 smooth, rounded whorls; P1 small. Primary spirals B and C appearing approximately simultaneously, C perhaps just slightly before B, as a pair of faint angulations on the lower ½ of the whorl, rapidly becoming distinct ribs. Primary A appearing within 0.5 whorl after B and C, achieving equal strength within 1.0 whorl, giving early whorls a subquadrate aspect. Secondary ribs appearing at about whorl 6–7. Sculpture on late whorls consisting of evenly spaced primaries and secondaries of approximately equal strength, separated by weaker intercalaries. Growth lines beginning to show marked positive relief at about whorl 3, producing axial costae particularly on subsutural shelf developed on early whorls between A spiral and suture. Beading caused by intersection of growth lines and spiral ribs persisting after whorl profile becomes rounded at about whorl 9–10. Teleoconch whorls wider than high, evenly rounded and somwhat inflated in profile. Area between C spiral and suture concave in profile. Lateral aspect of growth line trace orthocline to prosocline, with only lower inflection point. Sinus of moderate depth with apex just above whorl middle. Antispiral and basal sinues shallow.

Measurements.—See Table 30.

Stratigraphic and Geographic Distribution.—LA: Cook Mountain Formation; upper Claibornian Stage, Middle Eocene.

Type Locality.—Hammetts Branch, 2 mi NE of Mt. Lebanon, Bienville Parish, Louisiana (LA-BI-7).

Other Localities.—LA-BI-1 (B), LA-BI-2 (B), LA-BI-4 (B), LA-BI-5 (B), LA-BI-6 (B), LA-BI-8 (B), LA-CB-2 (B).

Type Material.—lectotype of *T. pleboides* Vaughan USNM 495175, paralectotypes USNM 147040.

Remarks/Discussion.—The apical sculpture places this form in the *mortoni* group and so in the genus *Palmerella*. Its convex whorl profile and shallow basal growth line sinus ally it with *P. femina* (Stenzel), although it shows finer sculpture than this Weches species.

Table 30.—Measurements of *Palmerella pleboides* (Vaughan). Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 495175 lectotype	7.0	22.0	9.5

Palmerella potomacensis
(Clark and Martin, 1901)
Plate 15, Figures 1,2

Turritella potomacensis Clark and Martin, 1901, p.149, pl.27, f.2,3; Clark and Miller, 1912, p.104,106,107, 119,120; Bowles, 1939, p.310; Stenzel and Turner, 1942, card 96; Palmer and Brann, 1966, p.1002.

Description.—Shell medium-sized, of 12–15 whorls. Maximum observed whorl diameter 11.5 mm. Apical angle approximately 12–15°, approximately equal to pleural angle. Sutures relatively deeply incised. Protoconch and earliest teleoconch whorls are unknown. Earliest known whorls (diameter = approx. 1.0 mm) showing two spirals of approximately equal strength in about middle of both upper and lower halves of whorl. Secondary spirals soon appearing. Basal spiral quickly becoming stronger and being joined by a second subequal spiral beneath it giving the whorls a basally carinate-cingulate appearance. Above basal carina, adult whorl surfaces covered with three to four principal spirals of approximately equal strength and an equal number of finer secondaries. Lateral aspect of growth line trace prosocline, with lower and upper inflection points very close to sutures. Sinus of moderate depth just below middle of whorl. Basal aspect of growth line trace unknown. Aperture unknown.

Measurements.—See Table 31.

Stratigraphic and Geographic Distribution.—VA: Nanjemoy Formation, Woodstock Member; Lower Eocene.

Type Locality.—1 mi. below Popes Creek, Charles County, Maryland (MD-CH-2).

Other Localities.—VA-KG-3 (B), VA-HA-2 (WD, MCZ).

Type Material.—2 syntypes of *T. potomacensis* Clark and Martin (plastic molds) USNM 207075, 207076.

Remarks/Discussion.—The earliest known spiral sculpture, as well as the profile of late whorls, of *potomacensis* are similar to those of *P. mortoni mortoni* from the underlying Aquia Formation. Although a well

Table 31.—Measurements of *Palmerella potomacensis* (Clark and Martin). Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 207075 syntype	8.0	35.0	12
USNM 207076 syntype	11.0	38.0	5.5

preserved apex is needed for confirmation, these features are sufficient to unite *potomacensis* with the *mortoni* group for the time being.

Palmerella sp.
Plate 11, Figure 5

Turritella sp. Ward, 1985, pl.4, f.12, 13.

Description.—Shell small to medium sized, of probably 10 to 15 whorls. Maximum observed whorl diameter 7.6 mm. Apical angle 20°; pleural angle may be slightly less than apical angle. Sutures indistinct on early whorls, only slightly incised on later whorls. Teleoconch whorls wider than high; early whorls straight-sided in profile, later whorls evenly rounded and convex. Protoconch and earliest apical whorls unknown. Earliest known whorls (dia. = 1.2 mm) bearing four spiral ribs. Two on lower ½ of whorl most prominent, located at around whorl midpoint and in middle of lower half, respectively. Next strongest on about middle of upper ½ of whorl, followed by one much weaker midway to upper suture. Lower two spirals remaining most prominent for several whorls, as intercalaries appear and come to equal strength with upper spirals. Profile of earliest whorls dominated by lower two ribs, upper ½ of whorl sloping straight down to them from the suture. Within approximately six whorls of earliest observed, whorl profile becoming evenly rounded as spirals assume more equal strengths, maximum diameter occurring in lower ⅓ of whorl. Sculpture on latest whorls consisting of approximately evenly spaced, equal strength, moderately pronounced spirals alternating with finer spirals. Sutures inconspicuous. Lateral aspect of growth line orthocline with weak upper and lower inflection points and moderately deep sinus with apex just above whorl middle. Antispiral and basal sinuses relatively shallow.

Measurements.—See Table 32.

Stratigraphic and Geographic Distribution.—VA: Nanjemoy Formation, Woodstock Member; Lower Eocene.

Localities.—VA-HA-3 (WD,MCZ), VA-HA-4 (WD,MCZ).

Remarks/Discussion.—This form appears to represent an undescribed species, but insufficient material is available to name it formally at this time. The earliest known spiral sculpture is similar to that of *Palmerella mortoni* and its close relatives, although a complete apex is required for positive determination. The whorl profile, adolescent and adult sculpture, and basal aspect of the growth line are most similar to those of *T. femina* from Gulf coast deposits of slightly later age.

Palmerella stenzeli, new species
Plate 11, Figures 9,10

Diagnosis.—Medium-sized turritellid with conspicuous, rounded basal carina, fine, even spiral sculpture and a depressed zone across the middle of the whorl.

Description.—Shell medium sized, of probably 15 to 20 whorls. Maximum observed whorl diameter 18.6 mm. Apical angle 17°; pleural angle slightly greater than apical angle. Sutures moderately deeply incised. Protoconch and earliest teleoconch whorls unknown. Smallest whorl examined (dia. = 0.14 mm, paratype MCZIP 29271) bearing three spirals of moderate strength, one on middle of upper ⅓ of whorl, one just below whorl middle and one on about middle of lower ⅓ of whorl. Lower two spirals slightly stronger than upper one, and lowest spiral forming edge of basal carina, below which whorl profile slightly concave. Secondaries of lesser strength appearing irregularly spaced between these spirals over next three to five whorls; original spirals decreasing in strength so that sculpture of later whorls consisting of numerous more or less equally spaced, equally fine spirals. Spirals not beaded. Whorl profile becoming increasingly basally carinate, basal carina becoming broader and rounded and comprising approximately lower ¼ of whorl. Middle of whorl becoming markedly concave between height of uppermost original spiral and carina. Lateral aspect of growth line trace orthocline to slightly prosocline, with only lower inflection point. Sinus moderately deep, with apex just above whorl middle. Antispiral nd basal sinuses moderately deep.

Measurements.—See Table 33.

Stratigraphic and Geographic Distribution.—TX: Kincaid Formation (Tehuacana Limestone); lower Midwayan Stage, Lower Paleocene.

Type Locality.—old Flat Rock Quarry, approx. 5 mi. S of Ola, Kaufman County, Texas (TX-KA-5).

Table 32.—Measurements of *Palmerella* sp. Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 366511	3.9	12.2	10.5
USNM 366512	5.9	14.4	4
MCZIP 29280	6.7	20.8	7.5
MCZIP 29280	7.6	20.3	6

Table 33.—Measurements of *Palmerella stenzeli* n. sp. Abbreviations as in Table 10.

	MD	*MH*	*WN*
MCZIP 29270 holotype	9.85	33.4	7.5
MCZIP 29272a paratype	12.0	34.0	10
MCZIP 29273a paratype	12.5	47.2	13
MCZIP 29273b paratype	13.0	44.2	11

Other Localities.—TX-LI-3 (MCZ).

Type Material.—holotype of *Palmerella stenzeli* n. sp. MCZIP 29270, paratypes MCZIP 29271, 29272, 29273, PRI 33198.

Etymology.—Named for the late H.B.Stenzel, pioneer of Texas Cenozic invertebrate paleontology.

Remarks/Discussion.—The sculpture of the earliest known whorls of this species most closely resembles that of *Palmerella levicunea* (Harris), for which the protoconch and earliest teleoconch whorls are also unknown. *P. stenzeli* is distinct from the other basally carinate Midwayan species of Texas (*P. hilli* (Gardner), "*Turritella*" *kincaidensis* Plummer, 1933 "*T.*" *plummeri* Stenzel and Turner, 1940) in its finer, unbeaded spiral sculpture and especially the medial concave band across the middle of later whorls. The type locality is close to that of "*T.*" *kincaidensis,* but the two forms have not been found together. *P. stenzeli* lacks the adapical concave constriction characteristic of "*T.*" *kincaidensis.* The prominent basal carina allies *P. stenzeli* with other similarly shaped lower Paleogene species of *Palmerella,* but, as for many species discussed here, definite supraspecific placement must await discovery of a well preserved apex.

This species is common to abundant in the dense limestones exposed at its two known localities. These limestones appear to belong to either the Tehuacana Member of the Kincaid Formation or to one or more of the limestone "lentils" of the underlying Pisgah Member.

Genus **HAUSTATOR** Montfort, 1810[6]

Type Species.—*H. gallious* Montfort, 1810 (= *Turritella imbricataria* Lamarck, 1804), Upper Eocene, England.

Diagnosis.—Shell medium-sized to vary large, of 15–25 whorls. Protoconch of 0.75 to 2.5 smooth, rounded whorls with small P1. Apical sculpture formula $C_1B_2A_3$. Profile of adult whorls round to basally carinate. Sculpture consisting of multiple simple, moderately developed spiral ribs. Apical angle less than or equal to pleural angle. Lateral sinus of the "*hybrida-imbricataria*" type, basal sinus moderate deep and simple.

Stratigraphic and Geographic Distribution.—U.S. Gulf and Atlantic Coastal Plains, Western Europe; Lower Paleocene—Upper Eocene.

Haustator alabamiensis
(Whitfield, 1865)
Plate 7, Figure 1–3

Turritella alabamiensis Whitfield, 1865, p.267; de Gregorio, 1890, p.128; Aldrich, 1894, p.239,246, pl.13, f.2; Harris, 1894b, p.30,48; 1896, p.109, pl.10, f.5; Gardner, 1935, p.284, in part; Bowles, 1939, p.299, pl.32, f.21; Stenzel and Turner, 1942, card 41; Palmer and Brann, 1966, p.979; Toulmin, 1977, p.173, pl.8, f.7; not Cossmann, 1893, p.29 under *tiga.*

Turritella mortoni Conrad. Smith and Johnson, 1887, p.59, in part; not Conrad, 1830.

Turritella alabamiensis var. *prealaba* Conrad. Kennedy, 1895, p.146, *nomen nudum.*

Turritella (*Haustator*) *alabamiensis* Whitfield. Cossmann, 1912, p.118.

Description.—Shell medium sized, of 15 to 20 whorls. Maximum observed whorl diameter 12 mm. Apical angle 20°; pleural angles slightly greater than apical angle. Sutures deep to shallow. Protoconch of 2.0–2.5 smooth rounded whorls; P1 unknown, probably small. Teleoconch whorls slightly wider than high, straight-sided to basally convex in profile. Apical sculpture formula C_1 B_2 A_3. Primary sprial C appearing as angulation on lower ⅓ of whorl, followed within approximately 0.5 whorl by primaries B and A, which quickly achieve equal strength with C. Primaries decreasing in relative strength, joined by numerous secondaries and tertiaries, so that whorls soon covered with evenly spaced, fine spirals of roughly equal strength. Primaries and secondaries may be faintly beaded on intermediate whorls. In most individuals, lower ¼ of whorl, bearing C spiral, becoming increasingly convex, eventually forming rounded but prominent angulation giving whorl a basally carinate form. Some specimens showing more concave whorl profiles with less pronounced development of basal carina. Lateral aspect of growth line trace orthocline or slightly prosocline, usually showing only lower inflection point. Lateral sinus moderately deep, with apex just above middle of whorl. Spiral and basal sinuses moderately deep.

Measurements.—See Table 34.

Stratigraphic and Geographic Distribution.—AL: Clayton Formation, Porters Creek Formation (Lower Member), Porters Creek Formation (Matthews Landing Member), Naheola Formation; GA: Clayton Formation, undifferentiated Midway Group; TX: Kincaid

[6] The name *Haustator* Montfort, 1810 is a junior subjective synonym of *Aculea* Perry, 1810 (Petit and Le Renard, 1990). In view of the widespread use of *Haustator,* however, Petit and Le Renard (1991) have proposed that it be conserved and that *Aculea* be suppressed. This was approved by ICZN Opinion 1677 (1992).

Table 34.—Measurements of *Haustator alabamiensis* (Whitfield). Abbreviations as in Table 10.

	MD	*MH*	*WN*
FMNH-UC 24522 syntype	10.0	35.0	11.5

Formation, Wills Point Formation?; AR: Porters Creek Formation; Midwayan Stage, Lower Paleocene.

Type Locality.—probably Matthews Landing, Alabama River, Wilcox County, Alabama (AL-WI-3).

Other Localities.—AL-WI-9 (B), AL-WI-16 (B), AL-WI-21 (B), AL-WI-24 (T), AL-WI-25 (T), AL-WI-36 (B), AL-WI-37 (B), AL-WI-38 (T), AL-WI-39 (T), AL-WI-40 (T), AL-WI-41 (T), AL-WI-42 (T), AL-WI-43 (T), AL-WI-44 (T), AL-WI-45 (T), AL-WI-46 (T), AL-WI-47 (T), AL-WI-48 (T), AL-WI-49 (T), AL-BU-1 (T), AL-BU-2 (T), AL-BU-3 (T), AL-HE-1 (T), AL-MA-2 (T), GA-RA-1 (T), GA-SL-2 (VS), TX-BA-30 (B), TX-BA-31 (B), TX-BA-32 (US), TX-CA-1 (B), TX-CA-3 (US), TX-FL-7 (B), TX-HU-1 (B), TX-KA-4 (B), TX-KA-1 (B), AR-PU-1 (PB).

Type Material.—11 syntypes of *T. alabamiensis* Whitfield FMNH-UC 24522.

Remarks/Discussion.—*Haustator alabamiensis* and "*Turritella*" *aldrichi* Bowles (see p.81) are often quite similar in their adult whorl shape and may be initially difficult to separate. These two species are very distinct in their early apical sculpture and whorl shape, however, and in the extremes of their adult whorl form as well. This similarity was discussed by Bowles (1939), who defended the separation of the two taxa "because of their apparent relationships to the latter well-established and distinct groups of *T.* [herein *Palmerella*] *mortoni* and *T. humerosa*."

Haustator carinata (I.Lea, 1833)
Plate 9, Figures 1–11

Turritella carinata I.Lea, 1833, p.129, pl.4, f.120; H.C.Lea, 1849, p.107; Dana, 1863, f.802; 1895, f.1486, copy 1863; Conrad, 1865a, p.32; 1866, p.11; de Gregorio, 1890, in part, pl. 11, f.3–5, f.6, copy I.Lea, 1833, f.9, copy *T. mortoni* Conrad, 1835a; not Heilprin, 1891, p.400; Cossmann, 1893, p.29; Harris, 1895b, p.10; Palmer, 1937, p.189, pl.24, f.5,6,8,9,12, pl.82, f.1; Bowles, 1939, p.304, pl.33, f.13; Stenzel and Turner, 1942, card 52; Brann and Kent, 1960, p.904, 905; Glibert, 1962, p.95. Palmer and Brann, 1966, p.983; not *T. carinata* H.C.Lea, 1841, p.96; not H.C.Lea, 1849, p.107 [= "*T*". *apita* de Gregorio]; Toulmin, 1977, p.301, pl.50, f.3; Dockery, 1980, p.81, pl.29, f.1.

Turritella mortoni Conrad. Conrad, 1835a, p.40, in part, pl.15, f.11 [Harris reprint 1893, p.40, pl.15, f.11]; not *T. mortoni* Conrad, 1830.

Turritella mortoni var. A Conrad, 1835a, p.40; not *T. mortoni* Conrad, 1830.

Turritella gracilis H.C.Lea, 1841, p.97, pl.1, f.12; 1849, p.107; de Gregorio, 1890, p.127, pl.11, f.32, copy I.Lea, 1833; Harris, 1895b, p.21.

Turritella monilifera H.C.Lea, 1841, p.97, pl.1, f.11; 1849, p.107; Harris, 1895b, p.29; not *T. monilifera* Adams and Reeve, 1848 (1850), p.48; not *T. monilifera* Deshayes, 1833, p.275.

Turritella mut. *tiga* de Gregorio, 1890, p.126, pl.11, f.22; Cossmann, 1893, p.29.

Turritella ghigna de Gregorio, 1890, p.125, pl.11, f.19; Palmer, 1937, p.191, pl.24, f.2,4,11,13,15, pl.83, f.1; Stenzel and Turner, 1942, card 65; Brann and Kent, 1960, p.914; Glibert, 1962, p.97; Palmer and Brann, 1966, p.988; Toulmin, 1977, p.302, pl.50, f.4.

Turritella litripa de Gregorio, 1890, p.125, pl.11, f.20.

Turritella carinifera claibornensis de Gregorio, 1890, p.126, pl.11, f.33, copy *T. monilifera* H.C.Lea, 1841.

Turritella hybrida Deshayes. de Gregorio, 1890, p.126, pl.11, f.23; not *T. hybrida* Deshayes, 1833, p.278.

Turritella eterina de Gregorio, 1890, p.126, pl.11, f.34–36; Cossmann, 1893, p.29.

Turritella claibornensis de Gregorio. Cossmann, 1893, p.29.

Turritella (*Haustator*) *claibornensis* de Gregorio. Cossmann, 1912, p.118.

Turritella (*Haustator*) *claibornensis tiga* de Gregorio. Cossmann, 1912, p.118.

Turritella (*Haustator*) *claibornensis eterina* de Gregorio. Cossmann, 1912, p.118.

Turritella mortoni turneri Palmer, 1937, p.194, pl.23, f.3,7; not *T. mortoni* Conrad, 1830; not *T. turneri* Plummer, 1933.

Turritella carinata palmerae Bowles, 1939, pl.33, f.12; Stenzel and Turner, 1942, card 61; Palmer and Brann, 1966, p.983–4; Toulmin, 1977, p.302, pl.50, f.1.

Description.—Shell medium sized to large, of 15 to 20 whorls. Maximum observed whorl diameter 18.6 mm. Apical angle 15°; pleural angle varying from approximately equal to apical angle to substantially greater. Sutures varying from faint to deeply incised. Protoconch suberect, homeostrophic, turbinate, of 0.75–1.25 smooth, somewhat flattened whorls; P1 small. Apical sculpture formula C_1 B_2 A_3. Primary C spiral appearing as angulation on lower ⅓–½ of whorl, followed after about 1.0 whorl by B spiral at about middle of whorl and closely associated with C. B and C quickly reaching equal strength and diverging. A spiral following B within about 0.5–0.75 whorls, quickly reaching equal strength with B and C. Very faint secondaries appearing between primaries beginning at whorls 8–9, becoming obsolete or persisting as very fine spirals, never as strong as primaries. Faint beading often present on primaries on intermediate whorls. Adult whorls slightly to very basally carinate, carina being formed by D spiral at basal angulation of whorl just above suture. Point of contact of a succeeding whorl may shift inward on base of preceeding whorl from margin of angulation, forming overhanging carina, or may remain close to margin, pleural angle remaining higher.

Measurements.—See Table 35.

Stratigraphic and Geographic Distribution.—AL: Gosport Sand, Upper Lisbon Formation; MS: Cook Mountain Formation; GA: McBean Formation[7], Lisbon Formation; SC: McBean Formation[7]; LA: Cook Mountain Formation; upper Claibornian State, Middle Eocene.

Type Locality.—Claiborne Bluff, Alabama River, Monroe County, Alabama (AL-MO-1a).

Other Localities.—AL-MO-4,b,c (P,B), AL-MO-11

[7] See Footnote 3, p.46.

Table 35.—Measurements of *Haustator carinata* (I.Lea). Abbreviations as in Table 10.

	MD	*MH*	*WN*
ANSP 5661 lectotype	11.6	22.0	3.5
ANSP 5662 syntype	9.4	28.1	7.5
ANSP 13174	3.2	17.1	12.0
ANSP 13175	5.5	15.2	8.5
PRI 2893	16.3	47.1	10.5
PRI 2889	11.1	21.8	4.5
PRI 2890	9.3	32.1	12.5
PRI 2891	20.0	30.2	2.0
MCZIP 29292	11.9	36.5	8.0
MCZIP 29293	16.0	48.5	8.0
MCZIP 29294	12.2	44.0	10.5
MCZIP 29296	18.0	44.3	6.0
MCZIP 29299	13.1	44.6	8.5

(T), AL-CL-4 (MCZ), AL-CH-9 (T), AL-WA-6(MCZ), MS-NE-1 (D,US), MS-NE-2 (P), MS-NE-3 (PB), MS-NE-7 (D), MS-NE-10 (US), MS-CL-1 (P,B), MS-CL-16 (B), MS-CL-17 (B), GA-BU-3 (VS), GA-TW-7 (VS), GA-HO-1 (VS), GA-HO-2 (VS), GA-SU-1 (VS), GA-RA-4 (VS), GA-GL-1 (VS), GA-WA-4 (VS), GA-WA-5 (VS), GA-WI-1 (VS), GA-JO-1 (VS), GA-BU-8 (VS), GA-BU-9 (VS), GA-BU-10 (ANS), GA-JF-1 (VS), GA-BI-1 (VS), SC-AI-1 (B), SC-OR-6 (B), SC-OR-7 (B), LA-WI-1 (B).

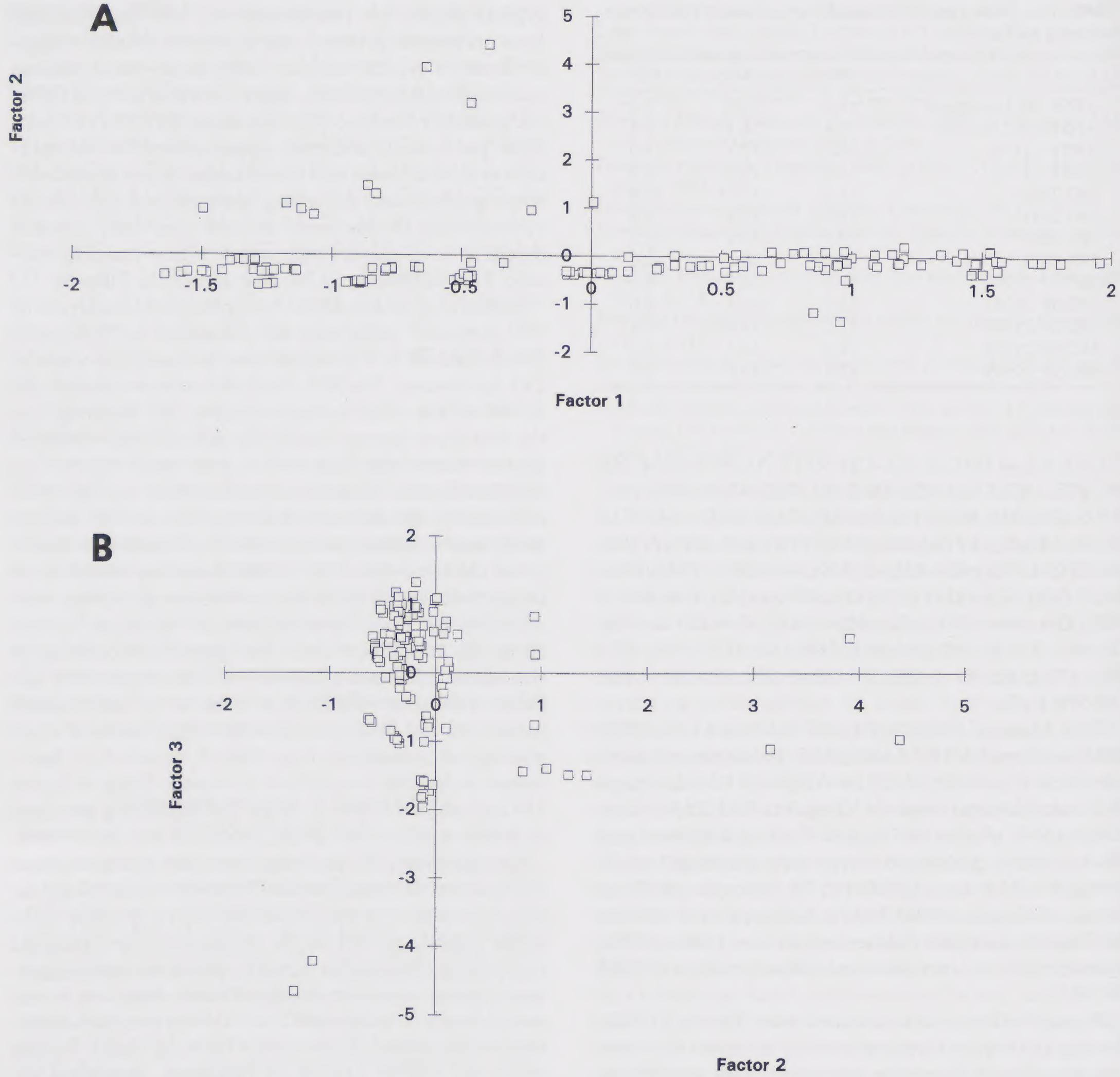
Type Material.—lectotype of *T. carinata* I.Lea ANSP 5661, syntypes ANSP 5662–5667; holotype and paratype ? of *T. gracilis* H.C.Lea ANSP 13174; holotype of *T. claibornensis tiga* de Gregorio PRI 26440; holotype of *T. ghigna* de Gregorio lost (*fide* Palmer and Brann, 1966, p.988); lectotype and paratype? of *T. monilifera* H.C.Lea ANSP 13175; holotype of *T. m. litripa* de Gregorio PRI 26441; holotype of *T. eterina* de Gregorio lost (*fide* Palmer and Brann, 1966, p.988); holotype of *T. carinata palmerae* Bowles USNM 497997.

Remarks/Discussion.—Stenzel and Turner (1942), Bowles (1939) and Palmer (1937) all note the variability within "*Turritella carinata*," and specifically that the forms designated as *Turritella ghigna* de Gregorio and *Turritella carinata* I.Lea intergrade in adult whorl form and sculpture. Palmer states that "When the intimate relation of the two lines of growth [i.e., *ghigna* and *carinata* lineages] is seen, one wonders if they are not dimorphic phases of the same species" (1937, p.189). Although she recognizes the two as separate species, for the sake of "taxonomic convenience," Palmer continues to refer to them as "phases" of a common stock.

Typical *ghigna* and typical *carinata* two forms differ (and intergrade) in both whorl shape and expression of spiral sculpture on the adult whorls; late whorls of typical *ghigna* are basally convex, but rounded, and bear prominent primary and secondary spirals, whereas those of typical *carinata* have sharp basal carinae and are generally smooth. Early whorls of the two forms are generally similar, although some forms of *carinata* show particularly attenuate upper spires. The intergradation in sculptural and whorl shape is in a qualitative sense gradual and complete, even among individuals co-occurring in the same sample, and fully justifies recognition of only a single, albeit highly variable, species. The variation can be seen clearly in Plate 9.

Results of multivariate morphometric analysis of "*T. carinata*" *sensu lato* are presented in Text-figure 20. A total of 117 variables was measured on each of 143 specimens. The first three factor axes account for 57.3% of the total variance (Table 36). Loadings on the first three factors (Table 37) indicate that variables on the fourth and fifth whorls load most heavily on the first factor, whereas variables from the eleventh and twelth whorls load most heavily on the second factor and variables on seventh whorl load most heavily on the third factor. It is clear from the distribution of specimens that there are no discrete groupings represented, but rather a continuum of variation, mostly along the first factor axis. The specimens plotting in the upper left hand quadrant of Text-figure 20A are those with later whorls (*i.e.*, whorls 11 and higher) perserved, but these also have the highly carinate morphology of *carinata* s.s. (*e.g.*, Plate 9, figures 6,7). Specimens assignable to *carinata palmerae* (Plate 9, figure 10) and *ghigna* (Plate 9, figure 3,4) fall along the right or positive side of the graph, along the first factor axis.

Qualitatively, *H. carinata* from the Gosport Sand differs from *H. rina* (Palmer) from the underlying Lisbon Formation in the persistence of its B spiral onto adult whorls, as well as the frequently more reduced expression of primaries A and C, which are quite prominent on late whorls in *H. rina.* If only these two forms were known, it might be reasonable to propose an ancestor-descendant relationship between them. Forms from the Upper Lisbon of Alabama, described by Bowles (1939) as "*Turritella carinata palmerae,*" and the equivalent Cook Mountain of Mississippi, figured by Dockery (1980), however, suggest that *H. carinata* originated well before the deposition of the Gosport, and that it showed a simlar range of variability early in its history as it did in the Gosport. "*T. c. palmerae*" is similar to the *ghigna* end of the Gosport *carinata* spectrum, whereas the Mississippi Cook Mountain specimens are close to the typical *carinata* form. Both "*T.*" *c. palmerae* and the Mississippi forms, however, are substantially smaller than the largest sizes of the Gosport specimens, suggesting a trend of increasing size within the lineage.



Text-figure 20.—Results of factor analysis of specimens of *Haustator carinata* (I. Lea). **A**. first and second factor axes. **B**. Second and third factor axes. See Appendix 1 for specimens used and details of analysis.

Table 36.—Results of factor analysis of specimens of *Haustator carinata* (I. Lea). Variance explained by first five factor axes.

Factor	*cumulative proportion of variance*
1	0.3082
2	0.4767
3	0.5725
4	0.6407
5	0.7015

Haustator cortezi (Bowles, 1939)
Plate 10, Figure 9

Turritella cortezi Bowles, 1939, p.280, pl.31, f.11,15; Stenzel and Turner, 1942, card 57; Palmer *in* Harris and Palmer, 1947, p.296–297; Palmer and Brann, 1966, p.985; Allison and Adegoke, 1969, p.1253.

Description.—Shell small to medium sized, of 10 to 15 whorls. Maximum observed whorl diameter 13.5

Table 37.—Results of factor analysis of specimens of *Haustator carinata* (I. Lea). Rotated factor loadings of each variable on each of the first three factor axes. Variables as indicated in Text-figure 3.

Variable	*factor 1*	*factor 2*	*factor 3*	Variable	*factor 1*	*factor 2*	*factor 3*
WH1	0.110	−0.152	−0.541	W2-7	0.330	−0.250	0.764
CH2-1	0.110	−0.151	−0.540	W3-7	0.344	−0.249	0.754
CH4-1	0.000	0.000	0.000	CW7	0.328	−0.251	0.765
SW1	0.109	−0.151	−0.536	CDC7	0.285	−0.249	0.784
W1-1	0.110	−0.152	−0.541	WH8	−0.385	−0.294	0.634
W2-1	0.110	−0.152	−0.541	CH2-8	−0.352	−0.293	0.611
W3-1	0.110	−0.152	−0.541	CH4-8	−0.431	−0.154	0.420
CW1	0.110	−0.152	−0.541	SW8	−0.446	−0.227	0.558
CDC1	0.110	−0.152	−0.541	W1-8	−0.398	−0.309	0.611
WH2	0.580	−0.111	−0.511	W2-8	−0.385	−0.310	0.608
CH2-2	0.578	−0.112	−0.520	W3-8	−0.375	−0.306	0.609
CH4-2	0.339	−0.045	−0.159	CW8	−0.382	−0.304	0.606
SW2	0.572	−0.100	−0.478	CDC8	−0.411	−0.303	0.612
W1-2	0.581	−0.109	−0.501	WH9	−0.738	−0.075	0.222
W2-2	0.581	−0.109	−0.501	CH2-9	−0.700	−0.079	0.208
W3-2	0.581	−0.109	−0.494	CH4-9	−0.622	−0.026	0.158
CW2	0.582	−0.108	−0.495	SW9	−0.689	−0.043	0.222
CDC2	0.581	−0.109	−0.496	W1-9	−0.754	−0.069	0.207
WH3	0.768	−0.112	−0.369	W2-9	−0.748	−0.062	0.208
CH2-3	0.720	−0.109	−0.356	W3-9	−0.745	−0.071	0.211
CH4-3	0.393	−0.047	−0.110	CW9	−0.751	−0.057	0.205
SW3	0.586	−0.060	−0.252	CDC9	−0.748	−0.053	0.213
W1-3	0.776	−0.110	−0.338	WH10	−0.630	0.318	−0.114
W2-3	0.777	−0.112	−0.350	CH2-10	−0.596	0.293	−0.120
W3-3	0.777	−0.112	−0.350	CH4-10	−0.534	0.320	−0.065
CW3	0.777	−0.112	−0.355	SW10	−0.582	0.344	−0.074
CDC3	0.773	−0.114	−0.349	W1-10	−0.641	0.355	−0.128
WH4	0.819	−0.034	−0.169	W2-10	−0.637	0.332	−0.134
CH2-4	0.794	−0.035	−0.178	W3-10	−0.637	0.332	−0.133
CH4-4	0.318	0.137	0.180	CW10	−0.638	0.344	−0.136
SW4	0.645	0.040	−0.047	CDC10	−0.633	0.344	−0.129
W1-4	0.816	−0.032	−0.156	WH11	−0.179	0.748	−0.050
W2-4	0.824	−0.035	−0.170	CH2-11	−0.182	0.736	−0.058
W3-4	0.828	−0.034	−0.169	CH4-11	−0.143	0.741	0.005
CW4	0.830	−0.038	−0.177	SW11	−0.174	0.788	−0.036
CDC4	0.816	−0.031	−0.156	W1-11	−0.185	0.755	−0.066
WH5	0.860	−0.063	0.068	W2-11	−0.185	0.767	−0.071
CH2-5	0.842	−0.069	0.047	W3-11	−0.184	0.763	−0.069
CH4-5	0.382	0.007	0.158	CW11	−0.182	0.769	−0.063
SW5	0.682	−0.017	0.127	CDC11	−0.178	0.757	−0.056
W1-5	0.850	−0.073	0.095	WH12	−0.062	0.830	−0.057
W2-5	0.862	−0.077	0.072	CH2-12	−0.059	0.840	−0.062
W3-5	0.867	−0.078	0.058	CH4-12	−0.071	0.620	−0.017
CW5	0.865	−0.082	0.063	SW12	−0.063	0.823	−0.046
CDC5	0.842	−0.072	0.085	W1-12	−0.057	0.856	−0.057
WH6	0.765	−0.180	0.319	W2-12	−0.055	0.856	−0.052
CH2-6	0.758	−0.182	0.288	W3-12	−0.058	0.848	−0.056
CH4-6	0.369	−0.074	0.354	CW12	−0.058	0.847	−0.057
SW6	0.486	−0.132	0.337	CDC12	−0.060	0.839	−0.056
W1-6	0.744	−0.187	0.343	WH13	0.007	0.674	0.023
W2-6	0.771	−0.190	0.306	CH2-13	0.007	0.674	0.023
W3-6	0.782	−0.191	0.297	CH4-13	0.007	0.674	0.023
CW6	0.770	−0.194	0.302	SW13	0.007	0.674	0.023
CDC6	0.731	−0.190	0.327	W1-13	0.007	0.674	0.023
WH7	0.340	−0.233	0.787	W2-13	0.007	0.674	0.023
CH2-7	0.349	−0.234	0.749	W3-13	0.007	0.674	0.023
CH4-7	0.078	−0.085	0.543	CW13	0.007	0.674	0.023
SW7	0.151	−0.180	0.703	CDC13	0.007	0.674	0.023
W1-7	0.302	−0.249	0.773				

Table 38.—Measurements *of Haustator cortezi* (Bowles). Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 495172 holotype	11.0	30.0	8.0
USNM 495173 paratype	9.0	22.0	6.0

mm. Apical angle approximately 15°; pleural angle increasing slightly until late whorls where it may decrease slightly; varying from approximately equal to apical angle to slightly greater. Sutures faint, not incised. Protoconch and earliest teleoconch whorls unknown. Earliest known whorls having A and C spirals equally prominent, with B spiral absent. A spiral expanding in later whorls to be much more prominent than C, making whorls adapically carinate, but may be again somewhat reduced on last whorl.

Measurements.—See Table 38.

Stratigraphic and Geographic Distribution.—MX, TX: Cook Mountain Formation; upper Claibornian Stage, Upper Eocene.

Type Locality.—near Mier, Tamaulipas, Mexico (MX-TA-1).

Other Localities.—TX-LA-1 (B), TX-LA-2 (B), TX-LA-3 (B), TX-LA-4 (B), TX-LA-5 (B), TX-ZA-2 (B), TX-ZA-3 (B), TX-ZA-4 (B), TX-ZA-5 (B).

Type Material.—holotype of *T. cortezi* Bowles USNM 495172, paratype USNM 495173.

Remarks/Discussion.—Based on the description given by Stenzel and Turner (1942), Allison and Adegoke (1969) suggest that the spiral ontogeny in this species is C_1 B_1 $a_1 \rightarrow$ d C_1 B_1 $A_1 \rightarrow$ d C_1 b_1 $A_1 \rightarrow$ d C_1 A_1, but add that the A spiral may appear after B and C. Without well preserved apices, however, the apical sculpture formula remains uncertain. If *cortezi* actually shows a pattern similar to other species in the *rina* group, it is probably most closely related to *Haustator subrina,* which also shows extreme development of primaries A and C; *cortezi* differs from *subrina* chiefly in its smaller size, greater apical angle and slightly reduced A relative to C on latest whorls.

Haustator fischeri
(Palmer *in* Richards and Palmer, 1953)
Plate 10, Figure 10

Turritella fischeri Palmer in Richards and Palmer, 1953, p.14, pl.1, f.1–3; Palmer and Brann, 1966, p.988; Allison and Adegoke, 1969, p.1253; Toulmin, 1977, p.335–6, pl.62, f.14.

Description.—Shell medium sized, of 15 to 20 whorls. Maximum observed whorl diameter 12.3 mm. Apical angle approximately 20°, approximately equal to pleural angle. Sutures shallowly incised on early whorls,

Table 39.—Measurements of *Haustator fischeri* (Palmer). Abbreviations as in Table 10.

	MD	*MH*	*WN*
FGS I 7399 holotype	15.1	39.3	5
FGS I 7400 paratype	6.2	19.4	15
FGS I 7401 paratype	13.0	31.0	6
FGS I 7402 paratype	14.8	58.9	12
FGS I 7403 paratype	14.0	34.0	5
FGS I 7400 topotype	16.8	27.9	3
FLMNH 19122 topotypes	12.5	40	8
	8.9	30	9

becoming slightly more deeply incised on later whorls. Protoconch and earliest teleoconch whorls unknown. Earliest known teleoconch whorls (1.2 mm dia.) showing A, B and C spirals, more or less equally developed. By about whorl 8–10, B spiral becoming weaker, continuing onto later whorls with whorl profile becoming cingulate and C spiral becoming stronger than A. D spiral visible only on later whorls, leading to slightly basally carinate shape of largest whorls. Secondary spirals consisting of one or two above A and one between A and B, visible by about whorl 8–10. C and D rarely equal in strength, forming cingulate band around base of whorl. Weathered specimens often appearing adapically carinate with rounded carina. Lateral aspect of growth line trace usually orthocline, with apex of lateral sinus just above middle of whorl. Basal growth line trace very simple.

Measurements.—See Table 39.

Stratigraphic and Geographic Distribution.—FL: Moody's Branch Formation (Inglis Member); lower Jacksonian Stage, Upper Eocene.

Type Locality.—pit N of town of Gulf Hammock, Levy County, Florida (FL-LE-1).

Other Localities.—FL-LE-2 (RP).

Type Material.—holotype of *T. fischeri* Palmer FGS I 7399, paratypes FGS I 7400–7403.

Remarks/Discussion.—Discussing the affinities of *Haustator fischeri,* Allison and Adegoke (1969, p.1254) suggest that the simultaneous reduction of the B spiral and strengthening of the D spiral "document the relation of this distinct species to *Turritella rina* subsp. *rina* Palmer."

Haustator gilberti (Bowles, 1939)
Plate 7, Figures 4,5

Turritella carinata I.Lea. Aldrich, 1894, p.235; Brantly, 1920, p.156; not *T. carinata* I.Lea,1833, p.129.
Turritella lineata I.Lea. Smith, Johnson and Langdon, 1894, p.156; not *T. lineata* I.Lea, 1833, p.130.
Turritella clevelandia Harris. Harris, 1897b, p.32; not 1894b, p.170.
Turritella clevelandia Harris var. Harris, 1899a, p.74, pl.10, f.2; Brann and Kent, 1960, p.907.

Table 40.—Measurements of *Haustator gilberti* (Bowles). Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 494993 holotype	10.0	35.5	11.5

Turritella gilberti Bowles, 1939, p.302, pl.32, f.16; Stenzel and Turner, 1942, card 66; Palmer *in* Harris and Palmer, 1947, p.291; Palmer and Brann, 1966, p.989; Toulmin, 1969, pl. 2, f.10; 1977, p.231–232, pl.29, f.7; Dockery, 1980, p.79–80, pl.2, f.2.

Description.—Shell small to medium sized, of 10 to 15 whorls. Maximum observed whorl diameter 9.6 mm. Apical angle 20°; apical and pleural angles approximately equal. Sutures moderately incised. Protoconch suberect, homeostrophic, turbinate, of 1.75–2.0 smooth, rounded, somewhat flattened whorls; P1 small. Apical sculpture formula C_1 B_2 A_3. Primary spiral C appearing as angulation just below middle of whorl, followed within about 0.5 whorls by primary B which appears just above C. Within next whorl B and C diverging until C lies in lower ⅓ of whorl and B just below whorl middle. Primary A appearing within 0.5 whorl after B and quickly attaining strength equal to B and C. Primary spirals and slight excavation between C spiral and suture giving succeeding teleoconch whorls tricarinate, subquadrate appearance. Secondary spirals appearing between primaries beginning around whorl 7 or 8, but remaining faint onto adult whorls. Lateral aspect of growth line trace orthocline or slightly prosocline with normally only lower inflection point. Lateral sinus moderately deep with apex above whorl middle. Spiral and basal sinuses moderately deep.

Measurements.—See Table 40.

Stratigraphic and Geographic Distribution.—AL, MS, GA: Bashi Formation; LA: Marthaville Formation; upper Sabinian Stage, Upper Paleocene-Lower Eocene.

Type Locality.—Woods Bluff, Tombigbee River, Clarke County, Alabama (AL-CL-2).

Other Localities.—AL-CL-1b (B), AL-CL-1c (B), AL-CL-1d (B), AL-CO-1 (B), AL-CO-2 (B), AL-DA-3 (US), AL-WA-2 (T), AL-BU-4 (T), AL-CL-7 (T), LA-NA-14 (L), MS-LA-3 (B), MS-LA-4 (B), GA-RA-3 (MCZ).

Type Material.—holotype of *T. gilberti* Bowles USNM 494993.

Remarks/Discussion.—There are at least two alternatives for the ancestry of *Haustator gilberti*; either it arose from *H. alabamiensis* (Whitfield), the only known Midwayan species with a C_1 B_2 A_3 apical sculpture formula, or from an as yet unknown form. Although a transition from *alabamiensis* to *gilberti* would have involved a size decrease, and this seems to have been generally uncommon in turritellid evolution, it seems the preferable choice considering the high fossil content of Wilcox and Midway Group units that seem to contain no other plausible ancestor.

Table 41.—Measurements of *Haustator infans* (Stenzel and Turner). Abbreviations as in Table 10.

	MD	*MH*	*WN*
TMM/TBEG 20955 syntype	2.5	8.5	9
TMM/TBEG 20956 syntype	2.8	9.3	10
TMM/TBEG 20957 syntype	3.0	8.5	9
TMM/TBEG 20958 syntype	3.7	10.5	11

Haustator infans
(Stenzel and Turner, 1940)
Plate 8, Figure 10

Turritella dumblei Harris n.var., Stenzel *in* Renick and Stenzel, 1931, p.102.

Turritella infans Stenzel and Turner, 1940, p.838, pl.47, f.12–15; 1942, card 71; Brann and Kent, 1960, p.921; Palmer and Brann, 1966, p.992.

Description.—Shell small to very small, known specimens of fewer than 10 whorls. Maximum observed whorl diameter 3.7 mm. Apical angle 19°; apical and pleural angles approximately equal. Sutures moderately incised. Protoconch suberect, homeostrophic, turbinate, of 1.5–2.0 smooth, slightly flattened whorls; P1 small. Teleoconch whorls wider than high, straight-sided to slightly rounded in profile. Apical sculpture formula C_1 B_2 A_3 or C_1 B_2 A_2. Primary spiral C appearing as angulation on lower ⅓ of whorl, followed 1.0–1.5 whorls later by A and B, which appear more or less simultaneously or B slightly earlier. C remaining strongest for 1–2 whorls then all three primaries attaining equal strength and remaining so, giving later whorls a tricarinate appearance. Secondary spirals appearing on approximately whorl 6–7. Area between C spiral and suture somewhat incised giving whorls a subquadrate form but base of whorl not concave so sutures not very profound in appearance.

Measurements.—See Table 41.

Stratigraphic and Geographic Distribution.—TX: Cook Mountain Formation (Wheelock Member), Stone City Beds; Claibornian Stage, Upper Eocene.

Type Locality.—"Moseley's Ferry", Stone City Bluff, Brazos River, Burleson County, Texas (TX-BU-1).

Other Localities.—TX-BU-2 (PB) ?

Type Material.—syntypes of *T. infans* Stenzel and Turner TMM/TBEG 20955, 20956, 20957, 20958.

Remarks/Discussion.—Stenzel and Turner note that faint beading is present on the spirals but I have not seen this on the syntypes. I have examined only the four syntypes, and only through the light microscope. The species is apparently rare in the fauna of the Stone City Beds, and appears genuinely to be a small species,

rather than just the young whorls of a larger form. Although examination of SEM is usually required for recognition of apical sculpture, the C spiral is prominent enough on the well preserved type specimens to recognize that it is the first to appear. How closely associated the appearances of A and B are must await SEM study of further material.

The early whorls of *H. infans* are very similar to those of *H. perdita* (Conrad) from the Upper Eocene Moody's Branch Formation of the central Gulf, showing both the same apical sculpture formula and flattened whorl shape. They differ chiefly in the apparently later appearance of primary spirals B and A, and the dissociation of B from C when it does appear. *Haustator gilberti* (Bowles) is almost certainly on the ancestral line of *infans*; the two form share small size, subquadrate whorl shape and tricarinate late whorl sculpture.

Haustator martinensis (Dall, 1892)
Plate 15, Figure 3

Turritella indenta var. *martinensis* Dall, 1892, p.308; Schuchert, Dall, Stanton and Bassler, 1905, p.677.
Turritella indenta Conrad. McCallie, 1908, p.357; not *T.indenta* Conrad, 1841.
Turritella martinensis Dall. Cooke, 1915, p.111; Bowles, 1939, p.282, pl.31, f.10; Stenzel and Turner, 1942, card 77; Palmer and Brann, 1966, p.993; Nicol, Shaak, and Hoganson, 1976, p.137ff, f.2.
Torcula martinensis martinensis (Dall). Allison and Adegoke, 1969, p.1263, pl.148, f.5.
Torcula martinensis henkeri Adegoke *in* Allison and Adegoke, 1969, p.1263–5, pl.147, f.2, pl.148, f.8,12, text-f.2,A,B,D,F,G.

Description.—Shell medium sized, of 15–20 whorls. Maximum observed whorl diameter 13.0 mm. Apical angle approximately 17°; pleural angle approximately equal. Sutures moderately incised. Protoconch and earliest teleoconch whorls unknown. Earliest known whorls showing A and C spirals more or less prominent. C spiral expanding with basal portion of whorl in later whorls, until whorls very slightly basally carinate. B spiral never more than faint thread on later whorls in middle of wide sulcus at mid-whorl. At least on other faint thread in sulcus on later whorls.

Measurements.—See Table 42.

Stratigraphic and Geographic Distribution.—FL: Crystal River Formation; GA?, MS?; Dept. Bolivar, Colombia; Middle to Upper Eocene.

Type Locality.—Martin Station, Marion County, Florida (FL-MA-1) (not Hernando County as often stated; Nicol *et al.*, 1976).

Other Localities.—FL-.

Type Material.—lectotype of *T. martinensis* Dall USNM 498390, syntypes USNM 112589, hypotype (Allison and Adegoke, 1969) UCMP 33743; holotype of *Torcula martinensis henkeri* Adegoke UCMP 32466, paratypes UCMP 32928, 32922, 32927, 32946, 32959, 32986, 33057.

Remarks/Discussion.—The stratigraphic and geographic distribution of this species have been unclear since its description. Allison and Adegoke (1969) consider records of the species from the Ocala Limestone and Barnwell Formation of Georgia (Bowles, 1939, p.283), the Forest Hills Sand of Mississippi (MacNeil, 1944, pp.1317,1326,1327), and Oligocene strata from Citrus County, Florida (Vernon, 1951, pp.166, 174–175) to be questionable, and perhaps assignable to other species such as *H. fisheri* (Palmer) or *H. subtilis* (Kellum). Chiefly on the basis of associated macrofossils, Allison and Adegoke believe *H. martinensis* from the type area to be of Oligocene age, possibly restricted to the Early Oligocene (assumed by MacNeil, 1944, 1946) who used the species as a guide fossil for this interval. Nicol *et al.* (1976), however, have pointed out that on the basis of microfaunas the limestones from the vicinity of Martin are of Late Eocene age and conclude that, whatever the age of putative occurrences elsewhere, *H. martinensis* in the type area is of Late Eocene age. They also note that this redetermination is consistent with the age of the subspecies ("*T. m. henkeri*") described by Adegoke (in Allison and Adegoke, 1969) from Middle to Upper Eocene deposits of Colombia.

Allison and Adegoke (1969) place *H. martinensis* in the genus *Torcula* Gray as its earliest known species, chiefly on the basis of its inferred apical sculpture formula, which they suggest is d C_1 b_3 A_2 based on the earliest observed teleoconch whorls. These authors are not specific about the ancestry of *H. martinensis,* but suggest (1969, p.1265) that some member of their "*Turritella rina* group" (= *Haustator* herein) is ancestral to *Torcula.*

Table 42.—Measurements of *Haustator martinensis* (Dall). Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 498390 lectotype	12.9	35.5	8.5

Haustator perdita (Conrad, 1865b)
Plate 8, Figure 1–9

Turritella perdita Conrad, 1865b, p.141, pl.10, f.10; 1866, p.11; Bowles, 1939, p.307, pl.32, f.11; Stenzel and Turner, 1942, card 90; Palmer *in* Harris and Palmer, 1947, p.292, pl.37, f.1-3,6,8–11; Brann and Kent, 1960, p.930–1; Palmer and Brann, 1966, p.1000; Dockery, 1977, p.45, pl.3, f.8,9; Toulmin, 1977, p.336, pl.62, f.11.
Turritella jacksonensis Cooke, 1926, p.136, f.8.
Turritella lowei Cooke, 1926, p.136, f.9.

Turritella perdita jacksonensis Cooke. Stenzel and Turner, 1942, card 72; Palmer *in* Harris and Palmer, 1947, p.294, pl.37, f.4,5,7,12, copy Cooke, 1926; Brann and Kent, 1960, p.931; Palmer and Brann, 1966, p.1001; Dockery, 1977, p.45, pl.3, f.7; 1980, p.82, pl.56, f.8,11,12.

Turritella perdita lowei Cooke. Stenzel and Turner, 1942, card 76.

Description.—Shell small to medium sized, of 15–20 whorls. Maximum observed whorl diameter 13.3 mm. Apical angle 16°; apical and pleural angles usually approximately equal, but pleural may be slightly greater. Sutures moderately incised. Protoconch suberect, homeostrophic, turbinate but slightly flattened, consisting of approximately 1.75–2.0 smooth, rounded whorls; P1 small. Teleoconch whorls wider than high, straight-sided to concave in profile. Apical sculpture formula C_1 B_2 A_3. Primary spiral C appearing as angulation just below middle of whorl and quickly becoming prominent. Primary B appearing 0.5–1.0 whorls later at or just above middle of whorl, at variable distance above C, and quickly achieving approximately equal strength. B and C immediately diverging until C lies in lower ⅓ of whorl and B at around middle. Primary A appearing in top ⅓ of whorl 0.5–1.0 whorls after B, and in most forms quickly becoming approximately equal in strength to B and C. Presence and strength of secondaries after appearance of A variable. Minor spirals may be limited to single weak secondaries between primaries or primaries decreasing in strength until entire whorl covered by numerous, evenly spaced, equally fine spirals. Primaries often showing minor beading on intermediate whorls. Beyond intermediate whorls, B spiral decreasing in strength, whorl width contracting between primaries A and C, giving later whorls a slightly concave profile. Primary C usually strongest on latest whorls of larger specimens. Area between C spiral and suture more or less excavated, giving whorls a subquadrate aspect. Lateral aspect of growth line trace orthocline to slightly prosocline, usually with upper and lower inflection points and moderately deep sinus whose apex may be above, below or on whorl middle. Spiral and basal sinuses of shallow to moderate depth.

Measurements.—See Table 43.

Stratigraphic and Geographic Distribution.—MS, LA: Moodys Branch Formation; lower Jacksonian Stage, Upper Eocene.

Type Locality.—*T. perdita* Conrad, Garland Creek, Clarke County, Mississippi (MS-CL-3); *T. p. jacksonensis* Cooke, *T. p. lowei* Cooke, Moody's Branch, Jackson, Hinds County, Mississippi (MS-HN-4).

Other Localities.—MS-CL-3 (B), MS-CL-15 (MCZ), MS-HN-1b (B), MS-HN-1e (B), MS-HN-3 (D), MS-HN-6 (D), MS-YZ-2 (D), LA-RA-3 (B), LA-GR-1 (D).

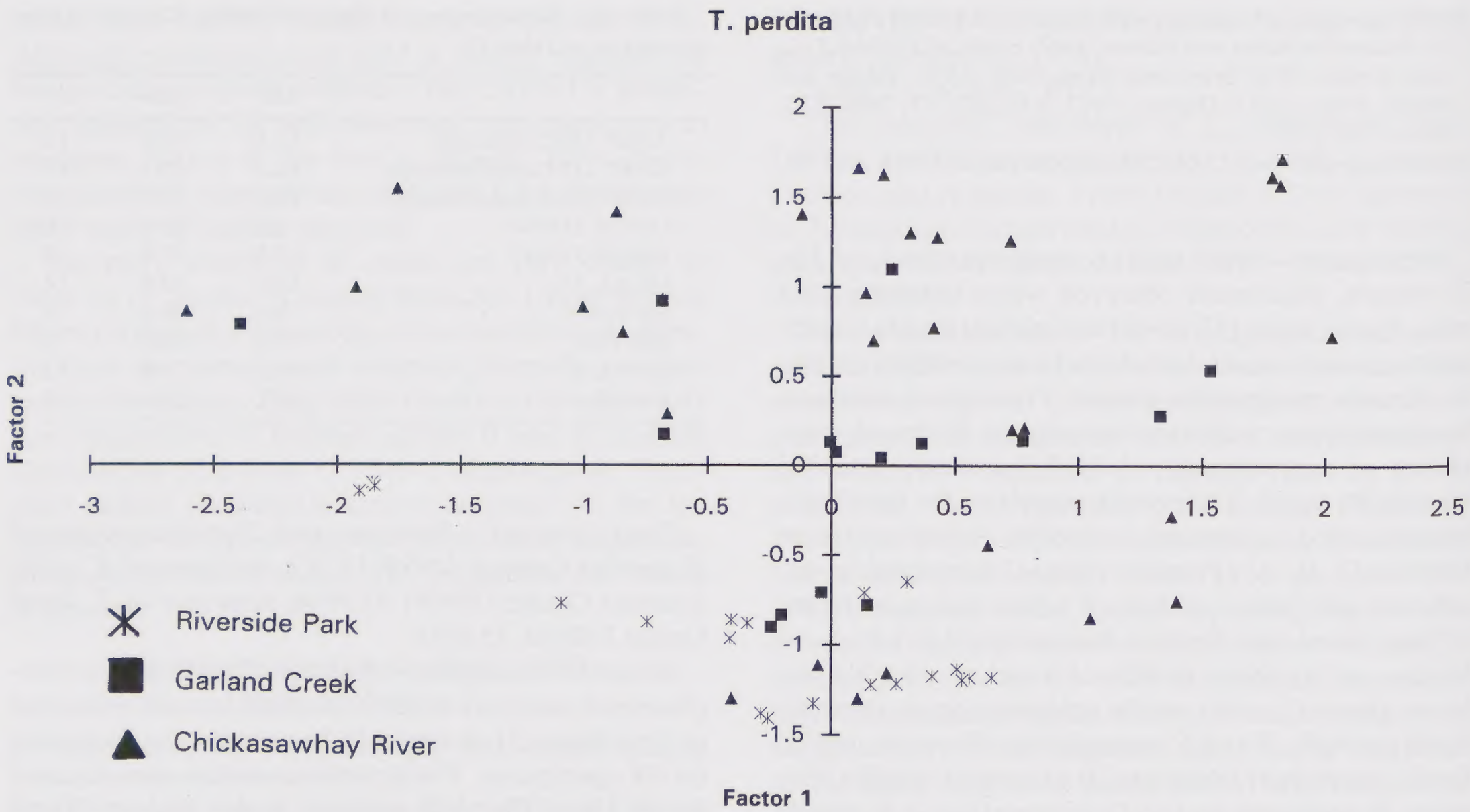
Table 43.—Measurements of *Haustator perdita* (Conrad). Abbreviations as in Table 10.

	MD	*MH*	*WN*
ANSP 13232 lectotype	12.3	41.3	13
ANSP 13232 paralectotype	10.5	35.1	10
ANSP 13232 paralectotype	10.6	37.6	10
USNM 353944	7.5	20.0	8
USNM 353945	7.5	23.0	8
MS-CL-15	13.3	45.0	14
MS-HN-3	8.6	25.0	9
MS-YZ-2	8.3	20.0	9
MS-CL-3	11.3	25.0	13
LA-GR-1	11.1	35.0	13

Type Material.—lectotype and 2 paralectotypes of *T. perdita* Conrad ANSP 13232; holotype of *T. jacksonensis* Cooke USNM 353944; holotype of *T. lowei* Cooke USNM 353945.

Remarks/Discussion.—Results of multivariate morphometric analysis on *perdita sensu lato* are presented in Text-figure 21. A total of 67 variables was measured on 68 specimens. The first three factor axes account for 60.1% of the total variance in the data set (Table 44). Loadings on the first three factors (Table 45) indicate that variables on the eighth, ninth and tenth whorls load most heavily on the first factor, whereas variables from the fifth and sixth whorls load most heavily on the second factor and variables on first and second whorls load most heavily on the third factor. It is clear from the distribution of specimens that there are no discrete groupings represented, but rather a continuum of variation, especially along axes representing variation on later whorls. In light of this pattern, there appears to be little justification for recognizing more than a single distinct taxon within *perdita.* There is, however, some degree of differentiation within *perdita* in the Moody's Branch Formation by locality. As indicated by the Measurements listed above, *H. perdita* from Clarke County is consistently larger than those from the Jackson area. Specimens from two localities in Clarke County in eastern Mississippi (Chickasawhay River and Garland Creek, MS-CL-15, MS-CL-3) show similar mean values but different amounts of variation, whereas specimens from 130 km to the east at Riverside Park in Jackson, in central Mississippi (MS-HN-6) shows a different mean and much less variation.

This variation may be due to environmental variation within the Moodys Branch sea. As discussed by Dockery (1977), and Hansen and Elder (1981), there is heterogeneity among depositional environments represented in the Moodys Branch Formation across its outcrop. Some of this variation is attributable to facies differences across roughly synchronous shelf en-



Text-figure 21.—Results of factor analysis of specimens of *Haustator perdita* (Conrad), first and second factor axes. * represents specimens from Riverside Park in Jackson, Hinds County, MS (locality MS-HN-6). ■ represents specimens from Garland Creek, Clarke County, MS (locality MS-CL-3). ▲ represents specimens from the Chickasawhay River, Clarke County, MS (locality MS-CL-15). See Appendix 1 for specimens used and details of analysis.

vironments, but some may also represent changes in environments through time. *H. perdita* appears to reflect this heterogeneity particularly well, showing a great variety of forms across its relatively restricted stratigraphic and geographic range. At the Town Creek locality in Jackson, Mississippi (MS-HN-3) *H. perdita* is the most abundant turritellid (Dockery, 1977, pers. comm.), whereas less than 6 km away at Riverside Park (MS-HN-6) *Palmerella alveata* (Conrad) is most abundant (pers. obs.).

Haustator rina (Palmer, 1937)
Plate 10, Figures 1,4,5

Turritella mortoni Conrad. Tuomey, 1848, p.159; not Conrad, 1830.
Turritella carinata I. Lea. Aldrich, 1886a in part, p. 46; not I. Lea, 1833.

Table 44.—Results of factor analysis of specimens of *Haustator perdita* (Conrad). Variance explained by first five factor axes.

Factor	*cumulative proportion of variance*
1	0.3051
2	0.4639
3	0.6010
4	0.6748
5	0.7417

Turritella carinata var. *praecarinata* Harris. Cooke, 1936, p.63, *nomen nudum*; not *T. praecarinata* Douvillé, 1904.
Turritella rina Palmer, 1937, p.192, pl.22, f.3,4,9; *in* Harris and Palmer, 1947, p.296; Bowles, 1939, p.277, pl.31, f.17; Stenzel and Turner, 1942, card 98; Brann and Kent, 1960, p.933,934; Glibert, 1962, p.99; Palmer and Brann, 1966, p.1003; Toulmin, 1977, p.305, pl.51, f.9; Dockery, 1980, p.79, pl.29, f.2,3,5,7.
Turritella rina carolina Palmer, 1937, p.194, pl.22, f.6; *in* Harris and Palmer, 1947, p.296; Bowles, 1939, p.280; Stenzel and Turner, 1942, card 53; Brann and Kent, 1960, p.934,935; Glibert, 1962, p.99; Palmer and Brann, 1966, p.1003; Allison and Adegoke, 1969, p.1257.
Turritella wechesensis Bowles, 1939, p.281, pl.31, f.8,14; Stenzel and Turner, 1942, card 108.
Turritella rina wechesensis Bowles. Palmer *in* Harris and Palmer, 1947, p.296; Palmer and Brann, 1966, p.1004.
Turritella rina rina Palmer. Allison and Adegoke, 1969, p.1256.
Turritella rina Palmer var. Dockery, 1980, p.79, pl.2, f.1.

Description.—Shell medium sized to large, of 15 to 20 whorls. Maximum observed whorl diameter 21.2 mm. Apical angle 18°; pleural angle usually greater than apical angle. Sutures deeply incised. Protoconch suberect, homeostrophic, turbinate, of approximately 1.75–2.0 smooth, rounded, somewhat flattened and inflated whorls; P1 small. Apical sculpture formula C_1 B_2 A_3. Primary spiral C appearing as faint angulation just below middle of whorl, followed within 0.5 whorl by B spiral just above C. B and C quickly diverging and

Table 45.—Results of factor analysis of specimens of *Haustator perdita* (Conrad). Rotated factor loadings of each variable on each of the first three factor axes. Variables as indicated in Text-figure 3.

Variable	*factor 1*	*factor 2*	*factor 3*	Variable	*factor 1*	*factor 2*	*factor 3*
WH1	−0.005	−0.089	0.794	W2-6	0.788	0.004	−0.146
SW1	−0.005	−0.089	0.794	W3-6	0.784	−0.052	−0.151
W1-1	−0.005	−0.089	0.794	CH6	0.773	−0.091	−0.150
W2-1	−0.005	−0.089	0.794	WH7	0.369	−0.050	−0.689
W3-1	−0.005	−0.089	0.794	SW7	0.087	−0.288	−0.511
CH1	−0.005	−0.089	0.794	W1-7	0.411	0.236	−0.632
WH2	0.335	−0.061	0.684	W2-7	0.417	0.184	−0.658
SW2	0.334	−0.079	0.615	W3-7	0.412	0.099	−0.672
W1-2	0.335	−0.059	0.689	CH7	0.392	0.077	−0.670
W2-2	0.341	−0.050	0.676	WH8	0.038	0.374	−0.101
W3-2	0.338	−0.056	0.682	SW8	−0.245	0.518	−0.236
CH2	0.339	−0.059	0.680	W1-8	−0.116	0.749	−0.215
WH3	0.648	−0.120	0.459	W2-8	−0.123	0.742	−0.227
SW3	0.606	−0.071	0.363	W3-8	−0.129	0.727	−0.229
W1-3	0.674	−0.053	0.448	CH8	−0.130	0.701	−0.225
W2-3	0.667	−0.083	0.441	WH9	−0.091	0.871	−0.139
W3-3	0.657	−0.101	0.447	SW9	−0.076	0.810	−0.148
CH3	0.659	−0.098	0.444	W1-9	−0.099	0.886	−0.128
WH4	−0.049	−0.160	−0.082	W2-9	−0.095	0.881	−0.134
SW4	0.617	−0.381	0.078	W3-9	−0.106	0.876	−0.133
W1-4	0.742	−0.223	0.195	CH9	−0.085	0.852	−0.125
W2-4	0.732	−0.260	0.176	WH10	−0.117	0.851	0.043
W3-4	0.730	−0.285	0.185	SW10	−0.025	0.803	0.028
CH4	0.724	−0.300	0.175	W1-10	−0.145	0.846	0.048
WH5	0.814	−0.238	−0.006	W2-10	−0.137	0.849	0.043
SW5	0.699	−0.310	−0.105	W3-10	−0.135	0.849	0.044
W1-5	0.838	−0.090	0.000	CH10	−0.107	0.836	0.048
W2-5	0.835	−0.124	−0.009	WH11	−0.324	0.523	0.035
W3-5	0.832	−0.160	−0.010	SW11	−0.286	0.507	0.029
CH5	0.828	−0.158	0.005	W1-11	−0.338	0.521	0.040
WH6	0.760	−0.160	−0.131	W2-11	−0.336	0.521	0.040
SW6	0.592	−0.145	−0.164	W3-11	−0.335	0.523	0.040
W1-6	0.786	0.064	−0.127				

B quickly becoming as strong or stronger than C. Primary A appearing on upper ⅓ of whorl within 0.25 whorl after B, but not reaching strength equal to C for three to four whorls by which point B becoming weaker. B rapidly becoming obsolete and disappearing by whorl 8–9. If present, secondaries very faint. Spirals A and C persisting at moderate strength throughout ontogeny, area between becoming concave. Whorl profile below C spiral and above suture usually relatively straight-sided leading to prominent D spiral. By about whorl 15, point of adapical contact between succeeding whorls beginning to move inward; D spiral becoming sharp and prominent basal carina. Lateral aspect of growth line trace slightly prosocline, usually with upper and lower inflection points and moderately deep lateral sinus with apex just above whorl middle. Spiral and basal sinuses moderately deep.

Measurements.–See Table 46.

Stratigraphic and Geographic Distribution.—H. rina s.s.: AL: Lower and Upper Lisbon Formation; MS, LA: Cook Mountain Formation; SC, GA: McBean Formation[8]; *H. rina carolina*: SC: McBean Formation[8]; *H. rina wechesensis*: TX: Weches Formation; Claibornian Stage, Middle Eocene.

Type Localities.—T. rina s.s.: Claiborne Bluff, Alabama River, Monroe County, Alabama (AL-MO-1b). *T. rina carolina*: Orangeburg County, South Carolina (SC-OR-1). *T. rina wechesensis*: well at Percilla, Houston County, Texas (TX-HO-13).

Other Localities.—T. rina s.s.: AL-MO-4 (B), AL-CL-13 (B), AL-CN-1 (B), MS-CL-1 (B), MS-CL-2 (B), MS-CL-16 (B), MS-CL-17 (B), MS-NE-1 (B), MS-NE-9

Table 46.—Measurements of *Haustator rina* (Palmer). Abbreviations as in Table 10.

	MD	*MH*	*WN*
PRI 2874 holotype	18.0	47.0	9.5
PRI 2868 paratype	10.0	25.0	7.5
MCZIP 29348	50.1	17.7	12.0

[8] See Footnote 3, p.46.

(B), MS-NE-10 (B), MS-NE-11 (B), LA-WI-1 (B), GA-BU-3 (B), SC-AI-1 (B), SC-LE-1 (B), SC-WI-1 (B); *T. r. wechesensis*: TX-RO-12 (B), TX-BA-3 (PB).

Type Material.—holotype of *T. rina* Palmer PRI 2874, paratypes PRI 2868, 2869; holotype of *T. rina carolina* Palmer PRI 2872; holotype of *T. rina wechesensis* USNM 497958 paratype USNM 497959.

Remarks/Discussion.—As already discussed, *Haustator rina* and *H. carinata* are very similar, both showing basal carination by expansion of the D spiral. Although it shows its first occurrence later than *H. rina, H. carinata* probably diverged independently from a common ancestor with *rina,* rather than from *rina* itself; it seems unlikely that a lineage would sharply reduce its B spiral, as *rina* and its close relatives do, and then give rise to a descendant with a better developed B, such as *carinata.*

Haustator rivurbana (Cooke, 1926)
Plate 10, Figure 3

Turritella rivurbana Cooke, 1926, p. 136, f.10; Bowles, 1939, p.283; Stenzel and Turner, 1942, card 99; Palmer *in* Harris and Palmer, 1947, p.295, pl.38, f.6,7,9, f.8, copy Cooke, 1926; Brann and Kent, 1960, p.935; Palmer and Brann, 1966, p.1004; Dockery, 1977, p.45–6, pl.3, f.6.

Turritella rivurbana rivurbana Cooke. Allison and Adegoke, 1969, p.1257–8.

Turritella rivurbana chiapasensis Allison *in* Allison and Adegoke, 1969, p.1258–9, pl.147, f.3,5,6,8–12,14, pl.148, f.2,11.

Turritella rivurbana mexicana Allison *in* Allison and Adegoke, 1969, p.1259–62, pl.147, f.4,13, pl.148, f.1,3,4,6,7,9,10,13,14.

Description.—Shell small to medium sized, of about 15 whorls. Maximum observed diameter approximately 8.6 mm. Apical angle approximately 20°; pleural angle approximately equal. Sutures moderately strongly incised. Protoconch and earliest teleoconch whorls unknown. Earliest known whorls showing A and C spirals with C spiral stronger. B spiral often present as thin thread, slightly closer to C than A. Sulcus between A and C spirals becoming broader with age. A and C staying very sharp and narrow, C always slightly stronger. Weak D spiral on later whorls forming a slight basal carination.

Measurements.—See Table 47.

Stratigraphic and Geographic Distribution.—MS: Moodys Branch Formation; lower Jacksonian Stage, Upper Eocene.

Table 47.—Measurements of *Haustator rivurbana* (Cooke). Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 353946 holotype	8.0	17.5	4.5
unnumbered MGS specimen	8.6	30.3	16.5

Type Locality.—Town Creek, Jackson, Hinds County, Mississippi (MS-HN-3).

Other Localities.—MS-HN-6 (D), MS-YZ-1 (B), MS-YZ-6 (B).

Type Material.—holotype of *T. rivurbana* Cooke USNM 353946; holotype of *T. rivurbana chiapacensis* Allison UCMP 12361, paratypes UCMP 30099, 30100, 31300, 32108, 32161, 32403, 32404, 32601, 32604, 32634; holotype of *T. rivurbana mexicana* Allison UCMP 30091, paratypes UCMP 32638, 32639, 32645, 32646, 32648, 32650. 32652, 32657, 32691, 32699, 32757, 32799.

Remarks/Discussion.—*H. rivurbana* is rare in the Moodys Branch Formation (pers. obs.; D.T.Dockery, pers. comm.). Allison and Adegoke (1969) have suggested that the Moodys is not the first occurrence of the species and have described a subspecies (*H. r. mexicana*) of "latest middle Eocene age" from near Simojovel, Chiapas, Mexico. These authors also, however, reiterate the suggestion of Palmer (*in* Harris and Palmer, 1947, p.296) that *rivurbana* is so similar to *H. rina* s.s., differing principally in size, that it may be conspecific with it, in which case the Mexican form would be a form of *H. rina* of approximately the same age. *H. rivurbana* is more similar to *H. martinensis* (Dall) than is *H. fischeri* (Palmer), and may be an intermediate form between Claibornian *rina* group species and the Upper Eocene to Recent genus *Torcula* Gray (cf., Allison and Adegoke, 1969).

Haustator subrina (Palmer, 1937)
Plate 10, Figure 2

Turritella eurynome Whitfield. Aldrich, 1894, p.233, not p.237; not Whitfield, 1865.

Turritella rina subrina Palmer, 1937, p.194, pl.22, f.1,2,5,7,8,10,11; Bowles, 1939, p.279, pl.31, f.16; Stenzel and Turner, 1942, card 103; Harris and Palmer, 1947, p.296; Brann and Kent, 1960, p. 934,935; Glibert, 1962, p.99; Palmer and Brann, 1966, p.1003, as *sabrina* [sic]; Allison and Adegoke, 1969, p.1257; Toulmin, 1977, p.305, pl.51, f.6.

Description.—Shell medium sized to large, probably of 15 to 20 whorls. Maximum observed whorl diameter 20.0 mm. Apical angle 23°; pleural angle usually slightly less than apical angle. Protoconch and earliest apical whorls unknown. Early ontogeny of spiral sculpture resembling that of *Haustator rina* (Palmer), but primary spirals A and C becoming more prominent more quickly; B often weakening and becoming obsolete earlier. Although C stronger than A on earlier whorls, A becoming stronger on later whorls, often expanding to form adapically flaring carina on upper ⅓ of whorl. Secondary spiral R becoming moderately prominent just below suture on late whorls, as does D, although not to degree shown in *H. rina.* Fine secondary visible

Table 48.—Measurements of *Haustator subrina* (Palmer). Abbreviations as in Table 10.

	MD	*MH*	*WN*
PRI 2866 syntype	15.0	17.0	2.0
PRI 2867 syntype	10.0	10.0	2.0
PRI 2870 syntype	22.0	68.0	6.0
PRI 2871 syntype	12.0	33.0	8.0
PRI 2875 syntype	14.0	41.0	8.0
USNM 495171	14.0	42.0	15.0
MCZIP 29304	20.9	58.8	8.5

below A spiral on late whorls. Growth line trace as in *H. rina,* except that lateral sinus may be somewhat deeper.

Measurements.—See Table 48.

Stratigraphic and Geographic Distribution.—AL: Upper and Lower Lisbon Formation; TX, MS: Cook Mountain Formation; SC: McBean Formation[9]; middle—upper Claibornian stage, Middle Eocene.

Type Locality.—1 mile S of Lisbon Landing, Alabama River, Monroe County, Alabama (AL-MO-4d).

Other Localities.—AL-MO-1b (B), AL-CL-13 (B), TX-HO-2 (B), TX-LE-12 (B), TX-SA-3 (PB), MS-NE-2 (PB), MS-CL-1 (PB), SC-OR-1 (PB), SC-OR-3 (PB), SC-OR-7 (PB).

Type Material.—syntypes of *T. rina subrina* Palmer PRI 2866, 2867, 2870, 2871, 2873, 2875.

Remarks/Discussion.—Although Palmer designated *subrina* as a subspecies of *Haustator rina,* she described it as morphologically distinct. This highly sculptured form in fact co-occurs with *H. rina* in the Lisbon and Cook Mountain formations without morphological intermediates. It is clearly closely related to *rina,* but its extreme development of primaries A and C, without the basal carination and development of D, distinguish it. The lack of intermediates between distinct co-occurring morphotypes argues for recognition of two separate species-level taxa.

Haustator subtilis (Kellum, 1926)
Plate 15, Figure 4

Turritella subtilis Kellum, 1926, p.27, pl.5, f.5; not Stephenson, 1927, p.21 [= *T. kellumi* Stephenson, 1939, fide Palmer and Brann, 1966]; Bowles, 1939, p.283; Stenzel and Turner, 1942, card 104, f.5; Palmer and Brann, 1966, p.1005.

Description.—Shell small to medium sized, of approximately 15 whorls. Apical angle approximately 15°; pleural angle approximately equal. Protoconch and earliest teleoconch whorls unknown. Sutures slightly incised. Earliest known whorls showing A,B and C

[9] See Footnote 3, p.46.

Table 49.—Measurements of *Haustator subtilis* (Kellum). Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 353240 holotype	7.0	24.0	10.0

spirals with C strongest and A and B of approximately equal strength. B spiral weakening to a fine thread and whorl becoming cingulate by whorl 6–8. Adult whorls not markedly carinate. Second, equally fine thread joining the B spiral on later whorls; two approximately equally spaced between the A and C spirals.

Measurements.—See Table 49.

Stratigraphic and Geographic Distribution.—NC: Castle Hayne Formation; Middle Eocene.

Type Locality.—city rock quarry near Smith Creek, E side of Wilmington, New Hanover County, North Carolina.

Other Localities.—known only from the type locality.

Type Material.—holotype of *T. subtilis* Kellum USNM 353240.

Remarks/Discussion.—This form is known from a single specimen, an external mold in glauconitic marl. Bowles (1939, p.283) suggests that it is closely related to *T. martinensis* Dall and to *T. rivurbana* Cooke, both of which are herein placed in *Haustator,* differing from these species in being "more slender and more gradually tapering . . ." and having whorls "marked by more prominent secondary lirae." Allison and Adegoke (1969) agree, and tentatively include it in their *rina* group. The holotype of *subtilis* differs from *martinensis* in having A and C spirals narrower, sharper and less pronounced, and the sulcus is accordingly shallower. The B spiral and faint secondaries in the sulcus are stronger than in *martinensis.*

Haustator tennesseensis (Gabb, 1860)
Plate 7, Figures 6–9

Turritella tennesseensis Gabb, 1860, p.392, pl.68, f.13; Harris, 1896, p.108, pl.11, f.5; Aldrich, 1921, p.25; Bowles, 1939, p.284, pl.32, f.12; Stenzel and Turner, 1942, card 105, f.5; Brann and Kent, 1960, p.938, Palmer and Brann, 1966, p.1005.
Turritella sp., Lowe, 1933, p.9.
Turritella mortoni Conrad. Lowe, 1933, p.10 in part, stations 6496 and 6497 only; not Conrad, 1830.

Description.—Shell small to medium sized, of 15 to 20 whorls. Maximum observed whorl diameter 9.5 mm. Apical angle 17°; apical and pleural angles approximately equal. Protoconch suberect, homeostrophic, turbinate but flattened, of about 2.5 smooth, rounded whorls; P1 small. Protoconch and earliest teleoconch whorls unusually tall, almost columnar, with

Table 50.—Measurements of *Haustator tennesseensis* (Gabb). Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 497989 hypotype	9.5	25.5	7.0

very small apical angle, increasing on around second or third teleoconch whorl. Apical sculpture formula C_1 B_1 A_2. Primary spirals B and C appearing approximately simultaneously on lower ½ of whorl, C as relatively sharp angulation just above suture and B as faint prominence just below whorl middle. B quickly becoming stronger, forming subcentral keel for several whorls. Primary A spiral appearing as faint ridge in middle of upper ½ of whorl. B soon surpassed by C as whorl profile changes to trapezoidal, widest on the bottom, then to hourglass-shaped as whorl middle constricts. Profile of latest whorls markedly concave, still slightly wider at the bottom. Spiral ribs greatly reduced in strength. Lateral aspect of growth line trace slightly prosocline, lacking well developed inflection points. Lateral sinus only of moderate depth. Basal aspect of growth line trace not observed.

Measurements.—See Table 50.

Stratigraphic and Geographic Distribution.—TN, MS: Clayton Formation; lower Midwayan Stage, Lower Paleocene.

Type Locality.—"Hardeman County, Tenn., marls of the Ripley Group" (Gabb, 1860).

Other Localities.—TN-HA-7a (B), TN-HA-7b (B), MS-TI-8 (B), MS-TI-9 (B), MS-TI-10 (B).

Type Material.—holotype of *T. tennesseensis* Gabb unknown (*fide* Bowles, 1939; Palmer and Brann, 1966, p.1005), hypotype (Bowles, 1939) USNM 497989.

Remarks/Discussion.—This species is allied with *Palmerella dutexata* (Harris) and *P. lisbonensis* (Bowles) in the "bicostate group" by Bowles (1939). Examination of early apical sculpture by SEM, however, suggests that its affinities lie with the "*T. rina* group" and that it should be placed in *Haustator*.

Haustator vaughani (Bowles, 1939)
Plate 15, Figure 5

Turritella vaughani Bowles, 1939, p.282, pl.32, f.14; Stenzel and Turner, 1942, card 107, f.14; Palmer and Brann, 1966, p.1006.

Description.—Shell very small, of 15–18? whorls. Largest observed whorl diameter 2.2 mm. Protoconch and earliest teleoconch whorls unknown. Apical angle approximately 10°; pleural angle approximately equal. Shell elongate, narrow and straight-sided. Earliest known whorls bearing only subequal, rounded A and C spirals, with no trace of B spiral. A becoming slightly stronger on later whorls; otherwise whorls gently curved, cingulate in profile. Very faint trace of one to two threads above A, at least one below C on later whorls. Sutures only slightly incised. Growth lines not visible.

Table 51.—Measurements of *Haustator vaughani* (Bowles). Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 497955 holotype	2.2	10.1	11.5

Measurements.—See Table 51.

Stratigraphic and Geographic Distribution.—SC: McBean Formation[10]; upper Claibornian Stage, Middle Eocene.

Type Locality.—Poosers Hill, 5.1 mi N of Orangeburg, Orangeburg, South Carolina (SC-OR-6).

Other Localities.—known only from the type locality.

Type Material.—holotype of *T. vaughani* Bowles USNM 497955.

Remarks/Discussion.—Commenting on the phylogenetic position of this species, Allison and Adegoke write: "The relationships of *Turritella vaughani* are in doubt. This species is known from only two specimens, the holotype and a topotype. Allison examined them and is of the opinion that they represent only portions of the juvenile whorls. The pleural angle of this species is extrmely narrow; the earliest whorls bear A and C with no sign of other ribs, although the earliest apical whorls and protoconch are missing. This species may have had an early tricostate or near tricostate stage, in which case it would belong to the *Turritella rina* group, but in the absence of the early apical whorls it is impossible to evaluate its relationships. It seems doubtful, however, that it belongs to *Torcula*" (1969, p.1262).

Genus ? ("*Turritella humerosa* group")

Remarks/Discussion.—Of all the species considered in detail in this paper, the least is known about those comprising the *humerosa* group. I have been able to find well preserved apices only for *Turritella aldrichi* Bowles, and sample size of several other species (*T. biboraensis* Gardner, *T. claytonensis* Bowles, *T. gardnerae* LeBlanc) are very small or preservation is poor (*T. toulmini,* new species). These species are united only by their distinctive whorl profile, a character believed to be prone to homoplasy, and so might not comprise a monophyletic group. Phylogenetic conclusions about these species are therefore especially difficult. The origins of the four larger Late Paleocene

[10] See Footnote 3, p.46.

species is the biggest mystery. As discussed in more detail in the descriptions below, *T. humerosa* differs from *multilira, praecincta* and *eurynome* in having a broad, rounded carina made up of several spiral ribs, whereas the carinae of the others is sharper and composed of only the expanded R secondary spiral rib. *T. humerosa* occurs only on the Atlantic coast, *T. multilira* Whitfield and *T. eurynome* Aldrich only on the Gulf coast, and *T. praecincta* Conrad in both areas.

In Maryland the Aquia Formation, containing *praecincta* and *humerosa,* is unconformably underlain by the Brightseat Formation containing the very similar *T.* "*prehumerosa*" Govoni (1983; Govoni and Hansen, in press). On the Gulf coast, the time represented by the unconformity between the Brightseat and Aquia appears to be represented by the highly fossiliferous Matthews Landing Marl Member of the Porters Creek Formation. This unit contains no *humerosa*-like forms other than *T. aldrichi.* It is possible that *humerosa* (and *praecincta*?) evolved from "*prehumerosa*" on the Atlantic coast, whereas *eurynome* and *multilira* (and *praecincta*?) arose from *aldrichi* on the Gulf coast. Alternatively, all three Gulf coast forms could have been derived from Atlantic coast ancestors, and *aldrichi* could have been a sterile branch, related or unrelated to the others. Given the data presently available, all that can be done at this point is to put forth these alternatives in the hope of future testing.

"Turritella" aldrichi Bowles, 1939
Plate 12, Figures 1–4

Turritella humerosa ? Conrad. Aldrich, 1886a, p.59; not Conrad, 1835b, p.340.
Turritella multilira Whitfield. Aldrich, 1886a, p.59; not Whitfield, 1865, p.266.
Turritella humerosa var. *multilira* Whitfield. Aldrich, 1894, p.246, pl.13, f.3 as *multileia* [sic]; Harris, 1896, p.111, pl.11, f.10, copy Aldrich, 1894.
Turritella humerosa Conrad var. Aldrich, 1894, p.246, pl. 13, f.5.
Turritella humerosa Conrad. Harris, 1896, p.111, in part, pl.11, f.11, copy Aldrich, 1894; Veatch and Stephenson, 1911, p.217, 219,223,224; Stephenson and Veatch, 1915, p.68–69; Brantly, 1920, p.145–146; not Conrad, 1835b.
Turritella aldrichi Bowles, 1939, p.315, pl.34,f.11,17; LeBlanc *in* Barry and LeBlanc, 1942, p.96, pl.13, f.3,4; Stenzel and Turner, 1942, card 42; Palmer and Brann, 1966, p.979–80; Toulmin, 1969, pl. 1, f.13; 1977, p.173, pl.8, f.10.

Description.—Shell medium sized, of 25 to 30 whorls. Maximum observed whorl diameter 11.1 mm. Apical angle 14°; apical and pleural angles approximately equal. Sutures inconspicuous on early whorls, more deeply incised on later whorls. Protoconch erect, homeostrophic, turbinate, of 1.0–1.5 smooth, rounded, somewhat flattened whorls; P1 small. Apical sculpture formula C_1 B_2 A_3. Primary C spiral appearing abruptly as distinct, raised band just below whorl middle, moving downward to middle of lower ½ of whorl. Primary B appearing within one whorl as less distinct prominence in middle of upper ½ of whorl, moving downward to just above middle of whorl. Primary A appearing as similarly faint prominence just below upper suture two to three whorls later, moving downward to middle of upper ¼ of whorl. Whorl profile becoming basally carinate with appearance of B spiral; area above C spiral relatively straight-sided, area below to suture sharply concave. Profile changing at about whorl 12–15 with appearance of secondary spiral (R) above A, R and A both increasing in size to form adapical carina on later whorls. Secondary spirals appearing over rest of whorl and strengthening to equal primaries B and C. Lower ⅔ of whorl swelling to become roundly convex; area just below adapical carina remaining somewhat constricted. Narrow band above lower suture becoming excavated and concave. Primary and secondary spirals on late whorls usually faintly to moderately beaded by intersection with growth lines. Lateral aspect of growth line trace slightly prosocline, with upper and lower inflection points and moderately deep sinus, apex just above whorl middle. Spiral and basal sinuses moderately deep.

Measurements.—See Table 51.

Stratigraphic and Geographic Distribution.—AL: Clayton Formation, Porters Creek Formation (Lower Member), Porters Creek Formation (Matthews Landing Member), Naheola Formation; GA: undifferentiated Midway Group; LA: Lime Hill ("Logansport") Formation; Midwayan Stage, Lower Paleocene.

Type Locality.—Matthews Landing, Alabama River, Wilcox County, Alabama (AL-WI-3).

Other Localities.—AL-WI-2 (T), AL-WI-3 (B), AL-WI-9 (B), AL-WI-21 (B), AL-WI-36 (B), AL-WI-37 (B), AL-WI-42 (T), AL-WI-43 (T), AL-WI-44 (T), AL-WI-45 (T), AL-WI-46 (T), AL-WI-47 (T), AL-WI-48 (T), AL-WI-50 (T), AL-WI-51 (T), AL-WI-52 (T), AL-WI-53 (T), AL-BU-1 (T), AL-BU-2 (T), AL-BU-3 (T), AL-MA-2 (T), LA-NA-6 (LB), GA-WE-1 (B), GA-SL-1 (B).

Type Material.—holotype of *T. aldrichi* Bowles USNM 495148, paratype USNM 495149.

Remarks/Discussion.—This is the only member of

Table 52.—Measurements of "*Turritella*" *aldrichi* Bowles. Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 495148 holotype	9.0	39.0	13.5
USNM 495149 paratype	10.0	41.0	9.5
MCZIP 29305	7.0	38.9	24.5

the *humerosa* group for which I have observed well preserved apices. "*T.*" *aldrichi* shares a common apical sculpture formula with members of the *rina* group (*Haustator* herein), but is distinguishable from the most similar member of that group, *Haustator alabamiensis* (Whitfield), by its very different spiral sculpture and whorl shape on early teleoconch whorls, and by distinct adapically carinate adult whorls in most individuals. As mentioned above under *H. alabamiensis,* however (p.67), some specimens of both species may be difficult to distinguish.

Whether *aldrichi* is closely related to any later members of the *humerosa* group is not clear. It differs from most of these species, as well as from most of the other adapically carinate Midwayan species ("*T.*" *claytonensis* Bowles, "*T.*" "*prehumerosa*" Govoni, "*T.*" *toulmini* n.sp., "*T.*" *biboraensis* Gardner) in being very small, delicate, narrow and having more than 20 whorls. It appears to persist virtually unchanged throughout much of the Midwayan Stage (perhaps as long as 7.0 my), and is perhaps best viewed as a more derived side branch than a generalized ancestral form.

At Matthews Landing on the Alabama River, *aldrichi* and *alabamiensis* are two of the most common mollusks, but in museum lots the two species occur in very different relative abundances. The exposures at Matthews Landing consist of continuously weathering horizontal bedding planes, and the differing composition of samples from here may suggest some microenvironmental heterogeneity of the original community.

"Turritella" biboraensis Gardner, 1935
Plate 14, Figure 5

Turritella biboraensis Gardner, 1935, p.290, pl.25, f.3; Stenzel and Turner, 1942, card 47.
Turritella sp. cf. *T. humerosa* Conrad. Gardner, 1935, p.289, pl.25, f.2.
Turritella humerosa biboraensis Gardner. Bowles, 1939, p.313; Palmer and Brann, 1966, p.991.

Description.—Available material very poorly preserved. Shell medium sized, total whorl number unknown. Maximum observed whorl diamter 15.9 mm. Apical angle approximately 10°?, approximately equal to pleural angle? Sutures moderately deeply incised. Protoconch and earliest teleoconch whorls unknown; earliest known whorls show pronounced, square adapical carina immediately below suture. Whorls straight-sided, marked with numerous, fine secondary spirals of more or less equal strength. May be slightly stronger spiral cord (C spiral?) at base of earliest whorls in holotype. Growth lines not visible on holotype.

Measurements.—See Table 53.

Stratigraphic and Geographic Distribution.—TX: Kincaid Formation; lower Midwayan Stage, Lower Paleocene.

Table 53.—Measurements of "*Turritella*" *biboraensis* (Gardner). Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 370989 holotype	15.9	42.4	5

Type Locality.—Bibora Tank, Indio Ranch, 18 mi SE of Eagle Pass, Maverick County, Texas (TX-MV-1).

Other Localities.—TX-LI-2a (B), TX-MV-4b (B), TX-MV-6 (B).

Type Material.—holotype of *T. biboraensis* Gardner USNM 370989.

Remarks/Discussion.—I have examined only the holotype of this species. It shares with "*T.*" *humerosa* Conrad a round, broad adapical carina and relatively straight whorl profile. It is distinguished chiefly on the basis of the substantial difference in the age of the two. Study of further material, particular well preserved apices, may show that such a taxonomic separation is not justified.

"Turritella" claytonensis Bowles, 1939
Plate 12, Figure 8

Turritella humerosa Conrad. Harris, 1896, p.110 in part, pl.11, f.12 only; not Conrad, 1835b.
Turritella claytonensis Bowles, 1939, p.314, pl.34, f.14,15; Stenzel and Turner,1942, card 55; Palmer and Brann, 1966, p.984.

Description.—Shell large, of perhaps 10–15 whorls? Maximum observed whorl diameter 26.0 mm. Apical angle approximately 15°, approximately equal to pleural angle. Protoconch and earliest teleoconch whorls unknown. Earliest known whorls show more or less uniform, fine spiral lines over entire whorl. Adapical carina develops on later whorls, probably from a secondary above the A spiral. Carina relatively narrow, subrounded, not more than 15% of whorl height; all other spirals faint. Sutures not incised, but perched immediately above carina. Basal portion of whorl immediately above suture slightly inflated. Lateral aspect of growth line trace approximately orthocline, with two inflection points, one above and one below whorl midpoint; lateral sinus of moderate depth. Basal aspect of growth line trace not observed.

Measurements.—See Table 54.

Table 54.—Measurements of "*Turritella*" *claytonensis* Bowles. Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 131637 holotype	26.0	68.0	7.5

Stratigraphic and Geographic Distribution.—AL: Clayton Formation; lower Midwayan Stage, Lower Paleocene.

Type Locality.—Prairie Creek, Wilcox County, Alabama (AL-WI-9).

Other Localities.—AL-BA-1 (B).

Type Material.—holotype of *T. claytonensis* Bowles USNM 131637.

Remarks/Discussion.—The USNM collections appear to contain only two specimens of this form, one (the holotype) from Prairie Creek in western Alabama, and the other from the type section of the Clayton Formation in eastern Alabama. I have found turritellids to be common at the Clayton type locality, but to consist entirely of the apparently undescribed species here named "*Turritella*" *toulmini*; I have not found any other specimens of "*T.*" *claytonensis*. The short spire and large apical angle make *"T." claytonensis* a very distinct form not easily confused with others; its rarity may therefore be real.

"Turritella" eurynome Whitfield, 1865
Plate 13, Figures 6–8

Turritella eurynome Whitfield, 1865, p.266; Aldrich, 1887, p.81; 1894, p.237, not p.233 [= *Haustator subrina* (Palmer)]; de-Gregorio, 1890, p.127; Harris, 1899a, p.75, pl.10, f.7; Bowles, 1939, p.292, pl.31, f.13, pl.32, f.18; LeBlanc *in* Barry and LeBlanc, 1942, p.97, pl.13, f.5; Stenzel and Turner, 1942, card 62; Palmer and Brann, 1966, p.987; Toulmin, 1977, p.231, pl.29, f.6.

Turritella bellifera Aldrich, 1885, p.150, pl.3, f.13; 1886a in part, p.34,55, pl.1, f.13, not 58; 1894 in part, p.237, not p.130,233,238; Smith and Johnson, 1887, p.29; not Clark, 1891, p.63; Cossmann, 1893, p.29; not Brantly, 1920, p.161; Plummer, 1933, p.815, pl.10, f.7; Bowles, 1939, p.317, pl.34, f.16; Stenzel and Turner, 1942, card 46; Palmer and Brann, 1966, p.982; Toulmin, 1977, p.230–1, pl.29, f.5.

Turritella (*Proto*) *cathedralis bellifera* Aldrich. de Gregorio, 1890, p.127, pl.11,f.17, copy Aldrich, 1885.

Turritella humerosa Conrad. Harris, 1899a, p.75, pl.10, f.5; 1899b, p.308, pl. 55, f.5; Brann and Kent, 1960, p.920; not Conrad, 1835b.

Turritella (*Haustator*) *bellifera* Aldrich. Cossmann, 1912, p.118.

Turritella sp., Plummer, 1933, p.815, pl.10, f.9,9a.

Turritella humerosa Conrad "var." Brann and Kent, 1960, p.920.

Description.—Shell large, of perhaps 15 to 20 whorls. Maximum observed whorl diameter 20.0 mm. Apical angle 15°, pleural angle 7°. Sutures inconspicuous. Protoconch and earliest teleoconch whorls unknown. Earliest whorls observed with three moderately prominent, approximately equally spaced spirals, the lower two soon becoming stronger as a fourth appears above the upper spiral, closer to the suture than the spiral. This uppermost spiral becoming most prominent on later whorls of most individuals, forming an adapical carina. Four spirals sharp and distinct on later whorls. Secondaries faint if present. Growth lines often conspicuous but spirals seldom beaded or scalloped. Whorl profile generally straight-sided until latest whorls when lower ½–⅔ of whorl becomes slightly rounded and convex. Lateral aspect of growth line trace slightly prosocline with well developed upper and lower inflection points. Lateral sinus moderately deep, apex above whorl midpoint. Spiral and basal sinuses of only moderate depth.

Table 55.—Measurements of "*Turritella*" *eurynome* Whitfield. Abbreviations as in Table 10.

	MD	*MH*	*WN*
FMNH-UC 24505 syntype	11.5	27.5	3.0
USNM 644614	17.5	85.0	11.5
USNM 498001	11.5	52.0	12.5

Measurements.—See Table 55.

Stratigraphic and Geographic Distribution.—AL: Tuscahoma Formation (Bells Landing Marl Member), Tuscahoma Formation (Greggs Landing Marl Member); LA: Marthaville Formation, Pendleton Formation; TX: Pendleton Formation; middle-upper Sabinian Stage, Upper Paleocene.

Type Locality.—*T. bellifera*: Bells Landing, Alabama River, Monroe County, Alabama (AL-MO-3); *T. eurynome*: Bowles (1939) believed it to be Bells Landing (AL-MO-3); Stenzel and Turner (1942) believed it to be Greggs Landing (AL-MO-5).

Other Localities.—AL-CH-6 (B), AL-DA-1 (B), AL-MO-3 (B), AL-MO-5 (ST,T), AL-WI-18 (B), AL-CH-6 (B), LA-NA-14 (LB), LA-SA-19 (LB), LA-SA-20 (WW), LA-SA-21 (WW), LA-SA-22 (WW), TX-SA-4 (LB), TX-SA-19 (LB).

Type Material.—lectotype of *T. bellifera* Aldrich USNM 644614; 3 syntypes of *T. eurynome* Whitfield FMNH-UC 24505.

Remarks/Discussion.—Bowles (1939) states that apical whorls of "*T.*" *eurynome* are "marked by three prominent subequal revolving lirae . . . a fourth lira arising just in front of the posterior suture very early in the shell growth . . . ," and that on adult whorls this fourth spiral occasionally "becomes strongly developed and approximates the prominent carina of *T. bellifera.*" Bowles also states that he did not observe the earliest apical whorls of *bellifera,* but that the earliest whorls known show "four distinct, subequal, revolving lirae and two smaller, less distinct secondary lirae," and that three versus four spirals on the earliest whorls distinguished the two species. The variability on both early and late whorls of specimens fitting the descriptions of these two forms suggests, however, that this separation cannot be maintained, especially considering the occurrence of both forms only in the Tus-

Table 56.—Measurements of "*Turritella*" *gardnerae* LeBlanc. Abbreviations as in Table 10.

	MD	*MH*	*WN*
LSU 3145 holotype	11.0	28.0	10.5

cahoma Formation (Bells and Greggs Landing Members). A single, somewhat variable species is therefore recognized here.

"Turritella" gardnerae
Le Blanc *in* Barry and LeBlanc, 1942

Turritella gardnerae Le Blanc *in* Barry and LeBlanc 1942, p.94, pl.13, f.1,2; Palmer and Brann, 1966, p.988.

Description.—Original description: "Spire probably high (incomplete holotype has only five whorls preserved), tapering very gradually; apical angle 9 degrees. Whorls wider than high, marked by a subsutural band or collar and depressed areas immediately below the subsutural band above the suture. Sutures are linear, indistinct and impressed slighly on the upper part of the subsutural band. Sculptural consisting of very numerous subequal fine and coarse spiral lines becoming larger but not prominent, anteriorly; spirals on depressed area above sutures and on subsutural band more prominent than elsewhere. Incrementals are strongly reflexed at the posterior third of the whorl as in the members of *Turritella humerosa* group." (LeBlanc, 1942, p.94) Protoconch and earliest teleoconch whorls unknown.

Measurements.—See Table 56.

Stratigraphic and Geographic Distribution.—LA: undifferentiated Upper Midway Group; Midwayan Stage, Lower Paleocene.

Type Locality.—Natchitoches Parish, Louisiana (LA-NA-6).

Other Localities.—LA-SA-9 ? (LB).

Type Material.—holotype *T. gardnerae* LeBlanc LSU 3145.

Remarks/Discussion.—According to LeBlanc, this species is known from only two localities. I have been unable to locate the type locality, and the second locality has been flooded by the waters of Toledo Bend Reservoir. "*Turritella*" *gardnerae* is most similar to "*T.*" *aldrichi* Bowles, although its status remains uncertain without additional material.

"Turritella" humerosa Conrad, 1835b
Plate 13, Figures 1–4

Turritella humerosa Conrad, 1835b, p.340, pl.13, f.3; 1846, p.219; 1865a, p.32; 1866, p.11 H.C.Lea, 1849, p.107; not Aldrich, 1886, p.59 [= "*T.*"*aldrichi* Bowles]; Harris, 1894a, p.303 in part; not 1896, p.15,16,32, 36,110, pl.11, f.10–13; not 1899a, p.75, pl.10, f.5–7; not 1899b, p.308, pl.55, f.5 [= "*T.*" *eurynome* Aldrich]; Clark, 1896, p.70, pl.14, f.1; Clark and Martin, 1901, p.148, pl.27, f.1,1a; not Veatch and Stephenson, 1911, p.217,219,223,224 [= *T. aldrichi* Bowles]; Clark and Miller, 1912, p.92,94,95,119,120; not Stephenson and Veatch, 1915, p.68,69 [= *T. aldrichi* Bowles]; Guillaume, 1924, p.290; Trowbridge, 1932, in part, pl.38, f.7, copy Clark and Martin, 1901; not pl.31, f.6,7; Gardner, 1935, p.288–290; Bowles, 1939, p.312, pl.33, f.10; Stenzel and Turner, 1942, card 70; Vokes, 1961, p.49, pl.10, f.2.

Turritella (*Haustator*) *humerosa* Conrad. Cossmann, 1912, p.118.

Not *Turritella humerosa* Conrad "var.". Cooke, 1926, pl.94, f.1 9 [= "*T.*" *multilira* Whitfield]; not Semmes, 1929, f.59–1, copy Cooke, 1926.

Turritella (*Peyrotia*) *humerosa* Conrad. Shimer and Shrock, 1944, p.493, pl.201, f.18, copy Clark and Martin, 1901.

Description.—Shell large to very large, of 20 to 25 whorls. Maximum observed whorl diameter 27.0 mm. Apical angle 17°; pleural angle often slightly less than apical angle. Protoconch unknown; earliest whorls observed (dia. = 0.34 mm) bearing two moderately pronounced spirals, probably corresponding to C and B, on lower ½ of whorl, moving slightly upward and strengthening until B just above whorl middle and C in about middle to lower ⅓ of whorl. Third spiral (= A?) appearing in middle of upper ½ of second whorl, but remaining weak. Lower two spirals subequal, C being slightly larger, forming moderate basal carina. Whorl profile above C more or less straight-sided except for spirals; profile below markedly concave to suture. Intercalaries appearing with whorl 10–12, largest whorls covered with numerous, evenly spaced, fine spirals. Whorl profile beginning to change well after introduction of secondary spirals, basal carina becoming less prominent, adapical ¼ of whorl beneath uppermost two spirals expanding, area just below becoming relatively constricted. Adult whorls showing rounded adapical carina just beneath the suture, slightly curved whorl profile widest at about middle of lower ½ of whorl. Spirals very seldom beaded although minor relief may be created by intersection of spirals and growth lines. Lateral aspect of growth line trace orthocline to slightly prosocline, usually with upper and lower inflection points. Lateral sinus moderately deep, apex just above whorl middle. Spiral and basal sinuses relatively shallow.

Measurements.—See Table 57.

Table 57.—Measurements of "*Turritella*" *humerosa* Conrad. Abbreviations as in Table 10.

	MD	*MH*	*WN*
ANSP 31388 lectotype	21.6	89.6	9.5
ANSP 31388 paratype	20.4	90.2	9.5
ANSP 31388 paratype	20.4	52.2	4.0
ANSP 31388 paratype	17.3	41.3	3.5
ANSP 31388 paratype	15.6	37.5	4.0

Stratigraphic and Geographic Distribution.—MD, VA: Aquia Formation; Upper Paleocene.

Type Locality.—probably Piscataway Creek, Prince Georges County, Maryland (MD-PG-5).

Other Localities.—MD-AA-5 (B), MD-PG-7 (B), MD-PG-10 (B), VA-ST-2 (B), VA-ST-4 (B), VA-ST-5 (B), VA-ST-6 (B), VA-HA-2 (MCZ).

Type Material.—lectotype and 4 paratypes of *T. humerosa* Conrad ANSP 31388.

Remarks/Discussion.—As noted by Bowles (1939) the adapical carina so characteristic of *humerosa* group species (and the principal character suggesting a close relationship among them) is somewhat different among the different species. In *humerosa* the carina is not formed by a single spiral rib, but by the swelling of a broad area just below the suture, on which the uppermost (presumably A) spiral is the most prominent. This carina may or may not be homologous with those of *eurynome, multilira* and *praecincta,* which form mainly from the expansion of a single spiral rib, specifically the secondary above the uppermost primary (therefore presumably R).

Although protoconchs and very earliest teleoconch whorls have not been preserved on the specimens available to me, it is almost certainly the case that "*T.*" *humerosa* shows an apical sculpture formula of C_1 B_2 A_3, similar to that seen in members of the *rina* group and by "*T.*" *aldrichi* Bowles. Spiller (1977) has noted that *humerosa* has three to four whorls, in its protoconch. If this is true, and if it applies to at least the other large Late Paleocene species with adapically carinate whorls it would suggest 1) that *aldrichi* is not closely related to *humerosa* group; 2) that *humerosa* group species may have had relatively longer intervals in the plankton, greater powers of dispersal, and reduced tendency for speciation, possibly explaining their lower species diversity compared to the basally carinate *rina* and *mortoni* groups which appear to have had only short planktonic larval stages; 3) many of the forms designated as "*humerosa*" from other areas of the New World may have been more closely related to Coastal Plain taxa than are, for example, forms assigned to *Palmerella mortoni,* which has also been used in a similar "catch-all" fashion, but which may have had lower powers of dispersal.

In the Aquia Formation, *humerosa* occurs in the same beds as *P. mortoni,* but is never as abundant. No ecological or environmental separation is detectable between the two forms.

"Turritella" multilira Whitfield, 1865
Plate 12, Figure 5, 9–11

Turritella multilira Whitfield, 1865, p.266; not Aldrich, 1886a, p.59 [= "*T.*" *aldrichi* Bowles]; not Aldrich, 1894, p.237,239 [= "*T.*" *aldrichi* Bowles, not "*T.*" *bellifera* Aldrich as in Bowles, 1939, p.316, *fide* Palmer and Brann, 1966, p.997]; Whitfield, 1899, p.177; Harris, 1899a, p.75, pl.10, f.6 [as *humerosa* "var."]; Bowles, 1939, p.316, pl.32, f.15, pl.34, f.19; Stenzel and Turner, 1942, card 84; LeBlanc *in* Barry and LeBlanc, 1942, p.102, pl.13, f.9; Palmer and Brann, 1966, p.997; Toulmin, 1977, p.232, pl.29, f.8.

Turritella bellifera Aldrich. Aldrich, 1886a in part, p.58; not, 1885.

Not *Turritella humerosa* Conrad var. *multilira* Whitfield. Aldrich, 1894, p.246, pl.13, f.3 as *multileia* [sic] [= "*T.*" *aldrichi* Bowles, not *T. bellifera* Aldrich as in Bowles, 1939, p.316]; Harris, 1896, p.111 in part, pl.11, f.10, copy Aldrich, 1894.

Turritella multilirata [sic] Whitfield. Whitfield, 1899, p.177; not Adams and Reeve, 1848 (1850), p.48. *Turritella humerosa* Conrad "var.". Cooke, 1926, pl.94, f.1; Semmes, 1929, f.59–1, copy Cooke, 1926; Brann and Kent, 1960, p.920 in part, No. 272.

Description.—Shell medium to large, of probably around 20 whorls. Maximum observed whorl diameter 20.0 mm. Apical angle 16°; pleural angle 9°. Sutures inconspicuous. Protoconch and earliest teleoconch whorls unknown. Earliest whorls observed (dia. = 1.9 mm) three prominent spirals of equal strength, approximately equally spaced over whorl height. Whorl profile of these early whorls convex and evenly rounded, maximum width in middle. Area between lowest spiral and suture excavated and smoothly concave. Weaker intercalaries beginning to appear between original spirals, whorl profile changing to more straight-sided, although area between each pair of stronger spirals slightly concave. Secondary spiral above upper original becoming increasingly prominent and forming sharp adapical carina on late whorls. Whorl profile of latest whorls more or less straight-sided, but with slight constriction just below carina and slight inflation at about whorl middle. Form and strength of carina variable; upper surface usually sloping upward to suture, but is less often horizontal from a more sharply apically bent carina. Carina rarely doubled by expansion of another more adapical spiral. Lateral aspect of growth line trace slightly prosocline, with upper and lower inflection points. Lateral sinus only moderately deep, apex above whorl middle. Spiral and basal sinuses relatively shallow.

Measurements.—See Table 58.

Stratigraphic and Geographic Distribution.—AL: Nanafalia Formation, Tuscahoma Formation (Bells Landing Member); LA: Pendleton Formation; MX: undifferentiated Wilcox Group; lower—middle Sabinian Stage, Upper Paleocene.

Table 58.—Measurements of "*Turritella*" *multilira* Whitfield. Abbreviations as in Table 10.

	MD	*MH*	*WN*
FMNH-UC 24521 syntype	11.0	43.5	8.0
USNM 498012	13.5	60.0	11.0

Type Locality.—Nanafalia Bluff, Marengo County, Alabama (*fide* Bowles, 1939) (AL-MA-1).

Other Localities.—AL-DA-1 (T), AL-PI-6 (T), AL-WI-55 (PB), LA-NA-16 (L), MX-NL-4 (B).

Type Material.—2 syntypes of *T. multilira* Whitfield FMNH-UC 24521.

Remarks/Discussion.—Although this species is reported by Bowles (1939) to be restricted to the Nanafalia Formation, I have collected a small number of specimens assignable to it from the Bells Landing Member of the overlying Tuscahoma Formation at Bells Landing. As Bowles noted, some specimens of *multilira* on which the primary spiral ribs are relatively well developed and the adapical carina is not may resemble individuals of "*T.*" *eurynome* Whitfield on which secondary spirals are relatively reduced and the adapical carina relatively pronounced, but such intermediates do not appear to be sufficiently common to suggest that only a single species is present.

Table 59.—Measurements of "*Turritella*" *praecincta praecincta*. Abbreviations as in Table 10.

	MD	*MH*	*WN*
USNM 497991 hypotype	28.0	92.3	12.5
MCZIP 29280	31.1	98.4	11.5
MCZIP 29281	28.8	78.0	8.0
MCZIP 29282	28.4	82.8	9.5

"Turritella" praecincta praecincta
Conrad, 1864
Plate 14, Figures 1–4, 6

Turritella praecincta Conrad, 1864, p.211; 1865a, p.32; 1866, p.11; Harris, 1897b, p.24, 29,31; 1899a, p.76 in part, pl.10, f.8; 1899b, p.308, pl.55, f.6; Guillaume, 1924, p.290; 1926, p.425; Cooke, 1926, p.94, f.3; Semmes, 1929, f.59–3; Bowles, 1939, p.318, pl.33, f.11; Stenzel and Turner, 1942, card 97; LeBlanc *in* Barry and LeBlanc, 1942, p.103, pl.13, f.10; Wassem and Wilbert, 1943, p.188, 189, 193, pl.31, f.7; Brann and Kent, 1960, p.933; Palmer and Brann, 1966, p.1002; Toulmin, 1969, pl. 1, f.18; 1977, p.233, pl.29, f.10,11.

Description.—Shell medium sized to large, of 15 to 25 whorls. Maximum observed whorl diameter 31.1 mm. Apical angle 19°; pleural angle 15°; pleural angle not as low on younger specimens. Sutures vary from inconspicuous to deeply incised. Protoconch and earliest teleoconch whorls unknown. Earliest whorls observed (dia. = 0.36 mm) bearing two moderately prominent spirals of approximately equal strength on lower ⅔ of whorl, a third, weaker spiral appearing within 1.0 whorl midway between this pair and upper suture and rapidly becoming as strong. At whorl diameter of 1.0–1.5 mm, a fourth spiral appearing between uppermost of original three and upper suture. Within seven to eight whorls this uppermost spiral becoming most prominent, forming a sharp adapical carina projecting laterally as far as the lowest spiral and producing straight-sided whorl profile. Upper surface of carina on earliest carinate whorls bearing numerous fine spirals and slopes up roof-like to suture. Underside of carina immediately concave. Faint intercalaries present on rest of whorl; original spirals remaining strong but not projecting. Lower margin of whorl slightly to markedly concave, flaring out to meet suture. Carina quickly increasing in width on later whorls, attenuating outward and often becoming undulatory and/or flared adapically, sometimes leaving suture in a deep groove. Base of whorl bears numerous prominent spirals. Lateral aspect of growth line trace prosocline, with well developed upper and lower inflection points. Lateral sinus moderately deep; spiral and basal sinuses relatively shallow.

Measurements.—See Table 59.

Stratigraphic and Geographic Distribution.—AL: Nanafalia Formation, Tuscahoma Formation (Bells Landing and Greggs Landing Members); LA: Pendleton Formation; Sabinian Stage, Upper Paleocene.

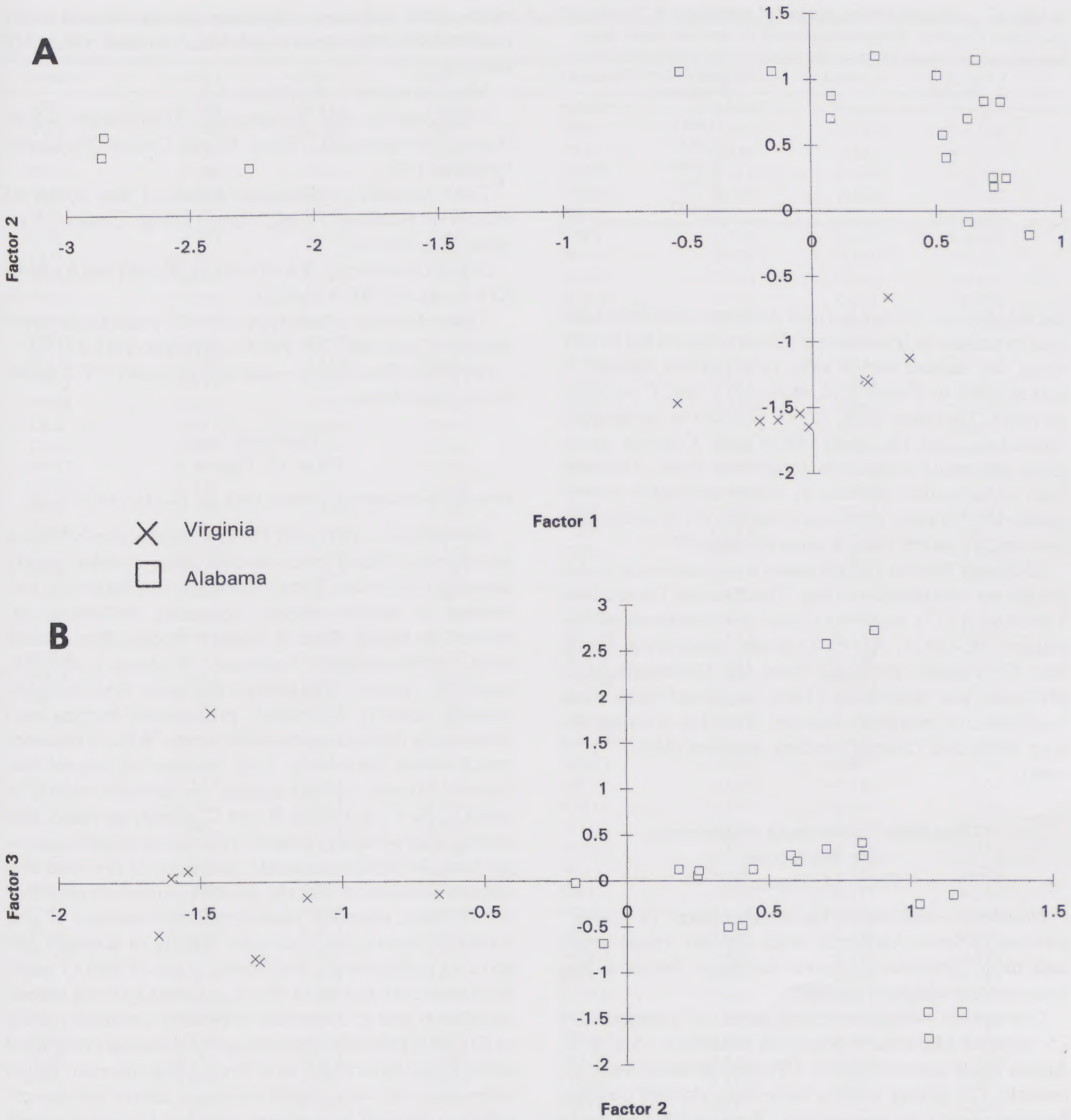
Type Locality.—unknown; given by Conrad as "Dallas Co., Alabama."

Other Localities.—AL-DA-1 (T), AL-PI-2 (T), AL-MO-3 (T), AL-MO-5 (T), AL-WI-1 (T), AL-WI-18 (B), AL-CH-6 (B), AL-CH-12 (T), TX-SA-4 (WW), LA-SA-21 (WW), GA-CL-4 (B).

Type Material.—holotype of *T. praecincta* Conrad unknown (*fide* Moore, 1962, p.89), hypotype (Bowles, 1939) USNM 497991.

Remarks/Discussion.—Prior to the work of Andrews (1971), the only published mention of "*T.*" *praecincta* outside the Gulf coast was a passing reference ("Va.: Aquia creek.") by Harris (1899a, p.76). Yet the sharply adapically carinate specimens from the middle of the Paspotansa Member of the Aquia Formation ("Bed E" in the scheme of Beauchamp [1984]) (Plate 14, Figure 4) of Maryland and Virginia are definitely not assignable to "*T.*" *humerosa* Conrad, and fall reasonably within the range of variation of "*T.*" *praecincta*. The Atlantic coast *praecincta* are smaller than their counterparts in Alabama, have smaller apical angles (around 15°), and show more pronounced spiral sculpture on the whorl below the carina, but they show the sharp, ledge-like, sometimes undulating and posteriorly flaring adapical carina distinctive of *praecincta* on the Gulf coast. The carina is never as extreme in the Aquia specimens as in *praecincta* from Alabama, but it is much more pronounced than in any other adapically carinate form, such as "*T.*" *multilira*.

These qualitative assessments are supported by the



Text-figure 22.—Results of factor analysis of specimens of "*Turritella*" *praecincta* Conrad. **A**. first and second factor axes. **B**. Second and third factor axes. × represents specimens from Virginia; □ represents specimens from Alabama (the type area). See Appendix 1 for specimens used and details of analysis.

results of the multivariate morphometric analyses (Text-figure 22). A total of 118 variables was measured on 28 specimens from Alabama and Virginia. The first three factor axes explain 76.8% of the variation in the total data set (Table 60). Loadings on the first three factors (Table 61) indicate that variables on the second and ninth whorls load most heavily on the first factor, whereas variables from the sixth and seventh whorls load most heavily on the second factor and variables on twelfth and thirteenth whorls load most heavily on

Table 60.—Results of factor analysis of specimens of "*Turritella*" *praecincta* (Conrad). Variance explained by first five factor axes.

Factor	*cumulative proportion of variance*
1	0.4018
2	0.5645
3	0.6396
4	0.7077
5	0.7553

the third factor. Virginina and Alabama specimens fall into two more or less distinct clusters, separated largely along the second factor axis, in a pattern similar to that showed by *Palmerella mortoni* s.s. and *P. m. postmortoni* (Text-figure 18, p.59). Given the geographic separation, and the observation that Virginia specimens are most similar to *praecincta* from Alabama than to any other species, it seems advisable to recognize the Virginia forms as a subspecies of *praecincta* (see below) rather than a separate species.

Although Bowles (1939) states that *praecincta* in Alabama is restricted to the Tuscahoma Formation, Toulmin (1977) reports at least two occurrences (localities AL-DA-1, AL-PI-1) in the underlying Nanafalia Formation, probably from the Grampian Hills Member. The specimens I have examined from these localities are markedly smaller than the average for later Bells and Greggs Landing samples (MD < 17.0 mm).

"Turritella" praecincta virginiensis,
new subspecies
Plate 14, Figure 4

Diagnosis.—Similar to but smaller than "*Turritella*" *praecincta* from Alabama, with smaller apical angle and more pronounced spiral sculpture below a less pronounced adapical carina.

Description.—Shell medium sized, of perhaps 10–25 whorls? Maximum observed diameter 16.9 mm. Apical angle approximately 15°, pleural angle approximately 12°, giving shell a somewhat domed outline. Sutures usually inconspicuous. Protoconch and early teleoconch whorls unknown. Earliest whorls observed (dia. = 9.8 mm) bearing faint adapical carina composed of several lesser spiral cords. Carina increasing in strength but remaining rounded to subquadrate in profile, and not expanding abapically down whorl. Whorls straight-sided below carina, surfaces covered with subequal spiral lines of fine to moderate strength. Base of whorl bears numerous prominent spirals. Lateral aspect of growth line trace prosocline, with well developed upper and lower inflection points. Lateral sinus moderately deep; spiral and basal sinuses relatively shallow.

Measurements.—See Table 62.

Stratigraphic and Geographic Distribution.—VA: Aquia Formation; SC: Black Mingo Group (Williamsburg Fm.) (?).

Type Locality.—Belvedere Beach, 1 km south of mouth of Potomac Creek, King George County, Virginia (VA-KG-5).

Other Localities.—VA-ST-4 (A), VA-ST-6 (A), VA-KG-5 (A), SC-BE-3 (MCZ).

Type Material.—holotype of "*T.*" *praecincta virginiensis* n. ssp. MCZIP 29093, paratype PRI 33199.

Remarks/Discussion.—See above under "*T.*" *praecincta praecincta.*

"*Turritella*" sp.
Plate 13, Figure 5

Torquesia prehumerosa Govoni, 1983, p.114–118, pl.5, f.11–15.

Description.—Govoni (1983) provides the following description: "Shell medium-size, long, slender, gently tapering turriculate. Suture narrowly but distinctly impressed in earlier whorls, becoming indistinct adpressed to nearly flush in mature whorls. Protoconch erect, homeostrophic, turbinate, of about 2 smooth, rounded, rapidly expanding volutions; first volution minute, initially depressed; protoconch merges into teleoconch without perceptible break. Whorls of teleoconch wider than high; total number of whorls unknown. Primary spirals appear on juvenile whorls in order a_3 B_2 C_1 d; spirals B and C quickly develop into strong, sharp-edged cords (C remaining slightly stronger than B) which dominate sculpture of juvenile and earliest adolescent whorls; spiral a initially forms low but distinct, rounded thread midway between B and posterior suture, but increases rapidly in strength relative to concurrently weakening cords B and C until, by about tenth to twelfth whorl, it forms a strong thread equal to b and c; d appears very early (probably prior to B) and forms a distinct though increasingly obscured spiral equal in strength to a. Over same interval, whorl sides become very slightly convex above gentle angulation formed by primary spiral c; by about eighth or ninth teleoconch whorl, fine secondary threads develop, first between spiral a and posterior suture and then in other interspaces below. With continuing addition and strengthening of threads in adolescent whorls, sides become more or less flattened except for very slight inflection between anterior suture and remnant of anterior angulation, and a posterior swelling which, in all but most mature whorls, forms a broad, low, rounded, though usually readily apparent subsu-

Table 61.—Results of factor analysis of specimens of "*Turritella*" *praecincta* (Conrad). Rotated factor loadings of each variable on each of the first three factor axes. Variables as described in Text-figure 3.

Variable	*factor 1*	*factor 2*	*factor 3*	Variable	*factor 1*	*factor 2*	*factor 3*
WH1	−0.789	0.144	0.046	W3-7	0.044	0.921	−0.007
SW1	−0.789	0.145	0.047	CR7	−0.004	0.915	0.028
CW1	−0.789	0.146	0.047	CD7	−0.256	0.834	−0.058
W1-1	−0.789	0.144	0.046	WW7	0.119	0.904	0.044
W2-1	−0.788	0.144	0.146	WH8	0.700	0.538	−0.150
W3-1	−0.787	0.143	0.045	SW8	0.712	0.575	−0.099
CR1	−0.788	0.146	0.047	CW8	0.701	0.603	−0.089
CD1	−0.697	0.138	0.046	W1-8	0.708	0.568	−0.116
WW1	−0.789	0.144	0.046	W2-8	0.710	0.565	−0.117
WH2	−0.908	0.158	−0.027	W3-8	0.701	0.561	−0.129
SW2	−0.906	0.158	−0.029	CR8	0.701	0.555	−0.075
CW2	−0.908	0.159	−0.027	CD8	0.596	0.614	−0.002
W1-2	−0.908	0.159	−0.027	WW8	0.710	0.574	−0.117
W2-2	−0.915	0.160	−0.021	WH9	0.931	−0.028	0.001
W3-2	−0.916	0.160	−0.020	SW9	0.940	0.069	−0.082
CR2	−0.917	0.161	−0.020	CW9	0.921	0.233	−0.051
CD2	−0.920	0.162	−0.005	W1-9	0.946	0.098	−0.091
WW2	−0.903	0.158	−0.030	W2-9	0.947	0.073	−0.085
WH3	−0.759	0.337	−0.309	W3-9	0.941	0.058	−0.095
SW3	−0.729	0.344	−0.330	CR9	0.924	0.011	0.067
CW3	−0.734	0.343	−0.325	CD9	0.733	0.486	−0.013
W1-3	−0.729	0.344	−0.329	WW9	0.940	0.072	−0.068
W2-3	−0.737	0.344	−0.323	WH10	0.819	−0.310	0.248
W3-3	−0.749	0.341	−0.318	SW10	0.852	−0.134	0.251
CR3	−0.768	0.337	−0.305	CW10	0.852	−0.014	0.254
CD3	−0.541	0.351	−0.375	W1-10	0.854	−0.143	0.221
WW3	−0.751	0.340	−0.317	W2-10	0.851	−0.162	0.229
WH4	−0.583	0.536	−0.402	W3-10	0.850	−0.167	0.228
SW4	−0.505	0.550	−0.416	CR10	0.824	−0.179	0.349
CW4	−0.514	0.547	−0.412	CD10	0.745	0.188	0.280
W1-4	−0.535	0.545	−0.411	WW10	0.856	−0.113	0.226
W2-4	−0.552	0.544	−0.409	WH11	0.805	−0.367	0.234
W3-4	−0.547	0.545	−0.411	SW11	0.849	−0.150	0.225
CR4	−0.546	0.543	−0.409	CW11	0.850	−0.061	0.221
CD4	−0.481	0.521	−0.385	W1-11	0.850	−0.164	0.219
WW4	−0.518	0.549	−0.415	W2-11	0.849	−0.169	0.211
WH5	−0.285	0.826	0.047	W3-11	0.846	−0.191	0.223
SW5	−0.234	0.837	0.064	CR11	0.823	−0.211	0.316
CW5	−0.235	0.837	0.067	CD11	0.753	0.101	0.185
W1-5	−0.254	0.835	0.071	WW11	0.852	−0.137	0.228
W2-5	−0.249	0.835	0.071	WH12	0.494	−0.070	0.576
W3-5	−0.264	0.834	0.077	SW12	0.535	0.038	0.546
CR5	−0.255	0.832	0.062	CW12	0.522	0.117	0.550
CD5	−0.292	0.796	0.040	W1-12	0.540	0.051	0.544
WW5	−0.219	0.833	0.071	W2-12	0.538	0.044	0.548
WH6	−0.113	0.924	0.005	W3-12	0.536	0.040	0.546
SW6	−0.045	0.927	0.056	CR12	0.514	0.021	0.607
CW6	−0.062	0.930	0.039	CD12	0.547	0.227	0.528
W1-6	−0.053	0.926	0.061	WW12	0.543	0.066	0.548
W2-6	−0.043	0.923	0.051	WH13	−0.047	0.003	0.817
W3-6	−0.044	0.917	0.059	SW13	−0.032	0.055	0.832
CR6	−0.084	0.921	0.017	CW13	−0.026	0.076	0.833
CD6	−0.189	0.849	−0.108	W1-13	−0.033	0.054	0.833
WW6	−0.026	0.920	0.077	W2-13	−0.032	0.054	0.833
WH7	−0.019	0.923	−0.011	W3-13	−0.035	0.047	0.832
SW7	0.069	0.914	0.061	CR13	−0.037	0.039	0.831
CW7	0.026	0.916	0.019	CD13	−0.016	0.107	0.807
W1-7	0.040	0.914	0.021	WW13	−0.029	0.063	0.830
W2-7	0.042	0.916	0.029				

Table 62.—Measurements of "*Turritella*" *praecincta virginiensis*. Abbreviations as in Table 10.

	MD	*MH*	*WN*
MCZIP 29093 holotype	16.9	56.3	9.0
MCZIP 29094	15.3	58.1	9.0

tural collar. The numerous fine, subequal spiral threads, numbering about 40 in largest preserved whorls, cover entire whorl surface including subsutural collar. Last whorl lacks obvious subsutural collar and exhibits a moderately strong, spiral thread-covered carina at the basal whorl angulation that apparently extends back from aperture onto penultimate whorl just above anterior suture; whorl base covered by numerous spiral threads. Growth lines indistinct, sinuous; acutely prosocline in upper third of whorl and steeply opisthocline below, forming a moderately deep spiral lateral sinus with vertex above midwhorl; slope increases in anterior third of whorl until, in lower fifth, slope increases very rapidly so that lines intersect suture at nearly right angle; recurved slightly on base angulation to form very shallow spiral arc on base. Aperture incompletely known; parietal region calloused."

Measurements.—See Table 63.

Stratigraphic and Geographic Distribution.—MD: Brightseat Formation; Lower Paleocene.

Type Locality.—bluff on Southwest Branch, just W of Capital Beltway, Prince Georges County, Maryland (MD-PG-12).

Other Localities.—MD-PG-13 (GO), MD-PG-14 (GO).

Type Material.—holotype and 20 paratypes of *Torquesia "prehumerosa"* Govoni USNM.

Remarks/Discussion.—Of all the adapically carinate species of Midwayan age, this form most closely resembles the Sabinan-age "*T.*" *humerosa* Conrad. Both species show a similar apical sculpture formula and form of the adapical carina, i.e., rounded and including more than a single spiral rib. Together with its geographic position, these characters make *prehumerosa* from the Brightseat a good candidate for a direct ancestor of *humerosa* from the Aquia (cf., Govoni, 1983).

Table 63.—Measurements of "*Turritella*" sp. ("*prehumerosa*" Govoni). Abbreviations as in Table 10.

	MD	*MH*	*WN*
holotype USNM	11.1	43.8	11
paratype USNM	9.1	29.6	5
paratype USNM	5.6	14.3	5
paratype USNM	1.4	4.4	8

"*T.*" *prehumerosa* is very similar to *biboraensis* Gardner, their geographic separation being perhaps the chief distinguishing feature. Govoni's form differs from "*T.*" *toulmini* n.sp. in having a relatively straight whorl profile below the carina. See Govoni and Hansen (in press) for further discussion.

"Turritella" toulmini, new species
Plate 12, Figure 6–7

Turritella humerosa Conrad. Toulmin, 1977, pl.8, f.6; not Conrad, 1835b.

Diagnosis.—Medium sized turritellid with a broad, rounded adapical carina, moderate, even spiral sculpture, and convex, slightly inflated whorl profile, widest around midwhorl.

Description.—Shell medium to large; total number of whorls unknown. Maximum observed whorl diameter 18.0 mm. Apical angle 10°; pleural angle may be slightly less than apical angle. Sutures inconspicuous. Protoconch and earliest teleoconch whorls unknown. Earliest teleoconch whorls observed on which sculptural detail is visible (dia. = 3.0 mm) showing at least three spirals, approximately evenly spaced over whorl, one at upper suture already forming an incipient adapical carina, one weaker near whorl middle, one in about middle of lower ½ of whorl. Whorls at this size straight-sided, approximately as high as wide. Spire attenuate, many-whorled. Numerous intercalary spirals appearing on succeeding whorls; sculpture of latest whorls consisting of approximately evenly spaced, equal strength spirals over upper ¾ of whorl, intercalated with one or more finer lines, and two to three stronger spirals on lower ¼. Whorl profile of late whorls convex over lower ¾ of whorl, widest point at about whorl middle, with a moderate constriction just below the pronounced, rounded, broad adapical carina. Lateral aspect of growth line trace orthocline, with well developed upper and lower inflection points and moderately deep sinus with apex just above whorl middle. Basal sinus unknown.

Measurements.—See Table 64.

Stratigraphic and Geographic Distribution.—AL: Clayton Formation; lower Midwayan Stage, Lower Paleocene.

Type Locality.—type section of Clayton Formation,

Table 64.—Measurements of "*Turritella*" *toulmini* n. sp. Abbreviations as in Table 10.

	MD	*MH*	*WN*
MCZIP 29274 holotype	14.6	55.0	8
MCZIP 29275 paratype	17.5	62.0	6

RR cut E of Clayton, Barbour County, Alabama (AL-BA-1).

Other Localities.—GA-CL-6 (T).

Type Material.—holotype of *T. toulmini* n. sp. MCZIP 29274, paratypes MCZIP 29275, 29276, PRI 33197.

Etymology.—Named for the late Lyman D. Toulmin, pioneer in Lower Tertiary stratigraphy and paleontology in the eastern Gulf Coastal Plain.

Remarks/Discussion.—At its type locality, "*T.*" *toulmini* is represented by silicified casts, together with molds in soft, yellow, sandy limestone which are readily studied by latex casts. This species is similar to "*T.*" *aldrichi* Bowles in its high, attenuate spire, but reaches a larger size and has a much more pronounced carina. In its rounded carina and subdued sculpture, "*T.*" *toulmini* most closely resembles "*T.*" "*prehumerosa*" Govoni (1983; Govoni and Hansen, in press), differing in its more inflated whorl profile below the carina and its larger maximum size, and could possibly rank as a subspecies of this form.

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APPENDIX 1

PROCEDURES USED IN MORPHOMETRIC ANALYSIS

Specimens of four fossil and one Recent turritellid species were measured with a video image analysis system. Digitized points and calculated measurements for these five species are shown in Text-figure 3. These measurements were divided into separate computer files, corresponding to separate samples (Table 65), and analyses began with these files. For each species, subsequent analysis followed these steps:

1) Each file was run separately through the computer program HISPIRE3 (Morris and Allmon, 1994), which aligns whorls of multiple specimens by comparing whorl heights.

HISPIRE3 aligns incomplete shells in three steps. In the first step, the program creates an array of whorl heights, in which rows are specimens and columns are whorls. It then sorts this array in order of increasing size of first (smallest) whorl. In the second step, the program steps through the rows (specimens) of the array and compares the heights of the first whorl of each pair of specimens. If a specimen has a first whorl of more than 0.8 of a whorl larger than the first whorl of the previous specimen, then blank whorls are added to its small end, and it is moved to the right in the array until it comes close to the size of a corresponding whorl in the previous specimen. This creates an array in which specimens are sorted in order of increasing size and are aligned by the sizes of their first whorls.

In the third step, HISPIRE3 iteratively a) finds the average height of each whorl in a composite average specimen in the array, b) applies up to three methods to move specimens to reduce the total error in the data set, and c) calculates the change in total error. The three methods are as follows. The specimen with the largest single error from the composite average is moved by one whorl to reduce its error (Method 1), then the specimen with the second largest errot is moved (Method 2), then the program steps down throught the specimens (from largest to smallest), and moves each specimen that is more than one whorl in error (Method 3). These iterations are repeated until the corrections produce an increase in the total error. This process is repeated until the number of passes is equal to ⅔ the number of specimens (a proportion arrived at empirically by experimenting with model data sets). One round of such iterations is called a "pass."

The three methods are used differently in different passes. Method 1 is used in each iteration of all passes. Method 2 is used in all but the last two passes. Method

Table 65.—Summary of samples used for morphometric analysis.

Species/sample	*locality*	*horizon*	*no. of specimens*	*no. of whorls*	*CV*
Palmerella mortoni					
MORTON2A	AL-MO-3	TSBL	4	8	7.43
MORTON2B	AL-MO-3	TSBL	8	8	6.23
MORTON2C	AL-MO-3	TSBL	11	9	7.63
MORTON2D	AL-MO-3	TSBL	6	9	6.08
MORTON2E	AL-MO-3	TSBL	9	10	6.23
MORTON2F	AL-MO-3	TSBL	32	9	7.82
MORTON2G	AL-MO-3	TSBL	17	9	6.87
MORTON2H	AL-MO-3	TSBL	15	8	8.71
MORTON3A	AL-MO-3	TSBL	23	9	7.61
MORTON3B	AL-MO-3	TSBL	17	11	9.74
MORTON3C	AL-MO-3	TSBL	12	10	7.26
MORTON4B	AL-MO-3	TSBL	18	9	9.32
MORTON4C	AL-MO-3	TSBL	23	10	7.96
MORTON6B	AL-MO-3	TSBL	3	8	7.54
MORTON7	AL-MA-1	NF	4	10	5.14
MORTON8	AL-MA-1	NF	9	8	6.40
MORTON9	AL-MO-5	TSGL	10	9	8.46
MORTON11	AL-WI-1	TSBL	23	10	7.16
MORTON12	AL-CH-7	NF	5	10	5.59
MORTON13	AL-DA-1	NF	8	11	4.52
MORTON15	AL-MO-3	TSBL	6	7	6.92
MORTON17	VA-KG-5	AQ	4	10	5.14
MORTON18	VA-KG-5	AQ	17	10	6.94
MORTON20	VA-KG-6	AQ	18	10	6.37
MORTON21	VA-KG-6	AQ	14	10	7.32
MORTON22	MD-PG-6	AQ	8	10	5.84
MORTON23	MD-PG-6	AQ	15	8	8.83
MORTON24	MD-PG-6	AQ	7	9	4.83
MORTON26	VA-KG-6	AQ	10	9	5.93
Haustator carinata					
CARINA2	AL-CL-4	GS	12	12	7.94
CARINA4	AL-CL-15	GS	12	8	4.15
CARINA6	AL-CL-4	GS	9	6	4.57
CARINA8	AL-MO-1	GS	4	8	4.78
CARINA9	AL-MO-11	GS	7	8	3.77
CARINA10	AL-CL-4	GS	7	6	5.15
CARINA11	AL-CL-15	GS	17	9	5.73
CARINA13	AL-CL-4	GS	11	9	6.94
CARINA14	AL-CL-4	GS	11	7	6.71
CARINA15	AL-WA-6	GS	8	7	6.83
CARINA17	AL-CL-14	GS?	10	8	4.99
CARINA18	AL-CL-14	GS?	12	9	6.49
CARINA19	AL-CL-14	GS?	8	8	4.27
CARINA20	AL-CL-15	GS	7	7	5.53
Haustator perdita					
PERDIT1	MS-HN-6	MB	15	9	8.10
PERDIT2	MS-CL-3	MB	8	9	5.24
PERDIT4	MS-HN-6	MB	16	7	8.17
PERDIT5	MS-HN-6	MB	4	6	4.94
PERDIT6	MS-CL-15	MB	8	7	5.73
PERDIT7	MS-CL-3	MB	8	8	5.74
PERDIT8A	MS-CL-15	MB	15	9	7.75
PERDIT8B	MS-CL-15	MB	14	10	6.77
"*Turritella*" *praecincta*					
PRAEC1	AL-MO-5	TSGL	9	9	7.25
PRAEC2	AL-MO-3	TSBL	11	12	5.92
PRAEC4	VA-ST-2	AQ	9	7	4.74
Turritella terebra					
TEREBR1	R-1		5	9	6.05
TEREBR2	R-2		3	12	3.10
TEREBR4	R-4		10	14	5.93
TEREBR9	R-5		9	13	5.77
TEREBR10	R-6		8	13	6.43
TEREBR18	R-2		8	14	7.23
TEREBR19	R-8		34	13	7.21

3 is used in passes 2 through n where n=½ the number of specimens in the sample.

Variations of this default alignment method work better in some data sets. The user can change the number of passes and thus the methods (1-3) used. If, however, the number of passes has been forced (by the user) to less than ⅓ the number of specimens, Method 3 is not used; if the number of passes has been forced (by the user) to some greater number of specimens, then Method 3 is used only in the second iteration.

These iterations produce a matrix of aligned specimens. In the final step this matrix is used to create the final data file from the original input data file, restoring specimens to their original order (but numbering them consecutively from 1; original numbering is lost unless specimen number is included as an additional variable). Missing whorl measurements are filled in this matrix with zeroes.

HISPIRE3 assays the accuracy of whorl alignments by checking the variation of heights for each whorl in the sample, and warns the user if this variation suggests poor alignments. The coefficient of variation (CV) is calculated for each aligned whorl and these values are then averaged across all whorls and again across all but the first and last whorls. Experience with the program suggests that if these two CV's are greater than 7-8%, the alignments of one or more specimens are likely to be incorrect by more than a full whorl.

In the initial runs, the default parameters of the program were used and CV's recorded.

2) For those files whose CV's exceeded 7%, a sequence of new analyses was performed. First, the number of passes was forced to ⅔ the number of specimens; then the number of passes was forced to less than ⅓ the number of specimens; then the number of passes was forced to twice the number of specimens.

3) For files whose CV's still exceeded 7%, graphs were made of aligned whorl number against whorl height. Specimens that still clearly lay outside the range of variation of the others were noted and these spec-

imens were manually adjusted by one whorl in either direction in the data file.

4) For one file, the range of variation in the whorl number/whorl height graph suggested that the specimens were all poorly aligned. This file (PERDIT1) was run through the program HISPIRE2, which aligns whorls by whorl expansion rate (W of Raup, 1966). See Morris and Allmon (1994) for further discussion.

5) Each data file had been run separately up to this point, yet single species were represented by many data files, and all of these now had to be aligned to each other. To do this, each separately aligned file was run through BMDP program 2D to calculate average values of whorl height for each whorl. The resulting values were assembled to form a composite average specimen representative of each file.

6) All composite average specimens for each species were grouped together and were now themselves run through HISPIRE3 in order to obtain alignment among the separate data files (i.e., samples) within each species. The results of this HISPIRE run were examined and the number of "empty" whorls (i.e., zeroes) added to the beginnings and/or ends of each composite was noted.

7) All files for each species were strung together in a new file, and the appropriate number number of empty whorls added to each file. The result was a single large data file for each species, in which specimens within samples and samples with each other had both been aligned by HISPIRE.

APPENDIX 2

Locality Register

Listed here are all localities given as occurrences for the turritellid species described in this paper. Some localities are redundant because of imprecise descriptions or changes in place names. One or more references are given when these have been available. Information on lithostratigraphic units from which fossils were collected is also included if known. When full descriptions of localities can be found in readily available sources such as Barry and LeBlanc (1942) and Toulmin (1977), I have only included their locality designation. References to collections following each locality are as follows: USGS—U.S.Geological Survey localities, listed in registry books deposited in U.S.National Museum; PRI—Paleontological Research Institution, Ithaca, NY; MGS—Mississippi Geological Survey; WA—locality from which I have collected personally. Page numbers on which each locality is cited are listed after the locality description.

ALABAMA

Barbour County

AL-BA-1 type locality of Clayton Fm., RR cut approx. 300 m north of Co. Hwy. 28, approx. 0.3 miles east of Clayton (86WA23; USGS 12164). pp. 83, 91

Butler County

AL-BU-1 Toulmin (1977) loc. Abu 1. pp. 68,81
AL-BU-2 Toulmin (1977) loc. Abu 6. pp. 68,81
AL-BU-3 Toulmin (1977) loc. Abu 11. pp. 68, 81
AL-BU-4 Toulmin (1977) loc. Abu 3. pp. 73

Choctaw County

AL-CH-6 Tuscahoma Landing, Tombigbee River; Tuscahoma Fm. incl. Bells Landing Marl (Toulmin, 1977, loc. ACh-2; USGS 5472). pp. 63, 83, 86
AL-CH-9 roadcut on Co. Hwy 21, approx. 1.3 miles south of Barrytown, 2.9 miles north of jct. with Hwy. 84, approx. 0.1 miles south of bridge over Souwilpa Creek, Coffeeville Lock and Dam 7.5 min. quad., T.10 N, R.3 W, sec 24; Upper Lisbon Fm. and Gosport Sand (?) (Toulmin, 1977, Loc. ACh-8; 85WA115). p. 69
AL-CH-11 road cut on Ala. Hwy 17, 6.7 mi N of Butler courthouse, sec 22 T 14 N, R 2 W; Bells Landing Mbr, Tuscahoma Fm. (Toulmin, 1977, loc. Ach12). p. 63
AL-CH-12 Toulmin (1977) loc. Ach20. pp. 63, 86

Clarke County

AL-CL-1 Choctaw Corner. p 73
1b 1¼ mi WSW of Choctaw Corner. p. 73
1c headwaters of Beaver Creek, approx. ¼ mi E of Choctaw Corners (USGS 7153, 7154). p. 73
1d "gully on land of Henry Jackson, near middle of sec 7, T 11 N, R 2 E, about 3 miles west of Choctaw Corners" (Bowles, 1939, p. 303) (USGS 7155). p. 73
AL-CL-2 Woods Bluff, left bank of Tombigbee River, sec 15, T 11 N, R 1 W; Bashi Fm. (Toulmin, 1977, loc. Acl2; USGS 262, 2667, 3099, 3100, 5470, 6205, 6206, 6207, 7482). p. 73
AL-CL-4 Little Stave Creek, approx. 3 mi. north of Jackson, approx. 0.75 mi. west of Hwy. 43, Jackson 7.5 min. quad. T.7 N, R.2 E, sec 20,29; Marianna Ls., Yazoo Fm., Moody's Branch Fm., Gosport Sand, Lisbon Fm., Tallahatta Fm. (83WA07,08, 85WA84). pp. 46, 69
AL-CL-7 road cut on east side of Ala. Hwy. 69, south side of Bashi Creek, 2.5 miles south of Marengo Co. line, 1.3 miles north of Campbell, T.11 N, R.1 E, sec 9 (Toulmin, 1977, Loc. Acl-1). p. 73
AL-CL-13 Coffeeville Landing, left bank Tombigbee River, Coffeeville 7.5 min. quad., R.1 W, T.9 N, sec 8,17 (Toulmin, 1977, Acl3) (85WA103, 86WA59; USGS 12181). pp. 77, 79
AL-CL-14 faulted blocks downstream from Coffeeville Landing, left bank Tombigbee River, Coffeeville 7.5 min. quad., section 17; Lisbon Fm. (83WA03,04, 85WA108, 86WA60). pp. 51, 54
AL-CL-16 between Alabama and Tombigbee Rivers, 1 mi SW of Rockville, 8.5 mi SE of Jackson (USGS 6157). p. 54

Coffee County

AL-CO-1 Elba Dam on Pea River; Bashi Fm. (Toulmin, 1977, ACof-1) (85WA114, 86WA45; USGS 10013, 10780). pp. 51, 72
AL-CO-2 near mouth of branch flowing into Pea River at Churchwells Branch, 5.5. mi S of Elba (USGS 10012, 10781.) . p. 73

Conecuh County

AL-CN-1 E side of Sepulga River on land of J.G.Robinson, sec 13, T 4 N, R 13 E (USGS 6737). pp. 54, 77

Dale County

AL-DA-1 Becks Mill (Munn's Mill), bed of Pea River, just upstream of Veterans Memorial Bridge (Hwy. 231), sec 7, T 7 N, R 23 E (Toulmin, 1977, Loc. Ada-2; 86WA41; USGS 10769). pp. 63,83, 86, 88

AL-DA-3 "hillside at swimming pool, near Atlantic Coast Line RR Station, Ozark" (Bowles, 1939,. p. 303); Bashi Fm. (USGS 11093). p. 73

AL-DA-4 shell bed in bank of Hurricane Creek, a southward flowing tributary of the Choctawatchee River, beneath bridge on Ala. Hwy 134 to Enterprise, approx. ¼ mi W of jct with old US Hwy. 231, sec 2 T 4 N, R 24 E; Bells Landing Mbr. p 63

Henry County

AL-HE-1 Toulmin (1977) loc. Ahe3. p.68

AL-HE-2 Toulmin and LaMoreaux (1963, p.399) bed 8 (Clayton Fm.), 80.7–80.4 mi above confluence of Flint and Chattahoochee Rivers, approx 8 mi above Ft. Gaines. p. 61

AL-HE-3 approx. 7 mi above Ft. Gaines, near Morris Landing (Veatch and Stephenson, 1911, p.220); Clayton Fm. p.61

AL-HE-4 Toulmin (1977) loc. Ahe1. p. 63

Marengo County

AL-MA-1 Nanafalia Landing, Tombigbee River, Pennington 7.5 min. quad., T.14 N, R.1 E, section 31 (USGS 271, 5641)

AL-MA-2 Toulmin (1977) loc. Ama-1; Porters Creek Fm.

Monroe County

AL-MO-1 Claiborne Landing and Bluff, left bank Alabama River, downstream from Hwy. 84 bridge at Claiborne, outcrops at water level and up steep bluff mostly overgrown except for occasional slumps, Claiborne 7.5 min. quad. T.7 N, R.5 E, section 25 (85WA95,96,97, 86WA57)

1a = Gosport Sand in bluff (USGS 263, 2391, 2867). pp. 46, 51, 68

1b = Upper Lisbon Fm. exposed at base of bluff on river bank (USGS 2395, 2396, 12171). pp. 54, 77, 79

AL-MO-3 Bell's Landing, left bank of Alabama River, Hybart 7.5 min. quad. T.10 N, R.6 E, sec 36; Bells Landing Marl Mbr., Tuscahoma Fm. (85WA85, 86WA55; USGS 260, 2669, 3098, 5593, 5594, 5595). pp. 63,83, 86

AL-MO-4 Lisbon Landing/Lisbon Bluff, right bank Alabama River, approx. 1 mi S of Claiborne Lock and Dam, Claiborne 7.5 min. quad., T.7 N, R.5 E, sec 3; Lower Lisbon Fm. (fide Toulmin, 1977) (85WA94; USGS 3105, 5511, 6086). pp. 68, 77

4b Lisbon Bluff, Bed 7 of Cooke section (USGS 13431, 14215). p. 68

4c Lisbon Bluff, Bed 4 of Cooke section (USGS 13433). p. 68

4d 1 mi S of Lisbon Landing. pp. 54, 79

AL-MO-5 Gregg's Landing, right bank Alabama River just downstream of island, Hybart 7.5 min. quad., T.10 N, R.6 E, sections 20, 29; Greggs Landing Marl Mbr., Tuscahoma Fm. (85WA86, 86WA56; USGS 268, 2670, 3117, 3118, 3604, 5642). pp. 63, 83, 86

AL-MO-11 Rattlesnake Bluff, left bank Alabama River, Claiborne 7.5 min. quad., T.7 N, R.5 E, section 31; Gosport Sand (83WA09, 85WA98). p. 68

Pike County

AL-PI-1 Three Notch Road., middle of sect. 17, T 8 N, R 20 E, ¼ mi NE of Henderson; Nanafalia Fm. (USGS 10765). pp. 63, 88

AL-PI-2 4.6-4.8 mi. north of Henderson on Co. Hwy. 21 (not marked—first right on entering Henderson from east on Hwy. 6) (Toulmin, 1977, Loc. Api-2?) (86WA42). p. 86

AL-PI-6 County hwy 3 in abandoned road bed on N side of paved road 1.0 mi NW of Henderson sec 7 T 8 N, R 20 E; Nanafalia Fm. (Toulmin (1977) loc. Api1). pp. 63, 86

Washington County

AL-WA-2 Hatchetigbee Bluff, right bank Tombigbee River at sharp bend, Tattlersville 7.5 min. quad., T.8 N, R.1 W, sections 17,38,20,21; type section, Hatchetigbee Fm. (Toulmin, 1977, Awa-1; 83WA05,06, 85WA100, 86WA61). p. 73

AL-WA-6 outcrop on Tombigbee River near Lone Star Cement Co. quarry, Tattlersville 7.5 min. quad., T.8 N, R.1 W, section 32; Gosport Sand (85WA101). p. 69

Wilcox County

AL-WI-1 Yellow Bluff, right bank Alabama River at sharp bend, Pine Hill 7.5 min. quad., T.11 N, R.6 E, sec 18,19 (Toulmin, 1977, Awi19; 85WA87; USGS 3121, 7480, 10782). pp. 63,86

AL-WI-2 1 mile west of Oak Hill (USGS 3107). p. 81

AL-WI-3 Matthew's Landing, right bank of Alabama River at bend, Lee Long Bridge 7.5 min. quad., T.12 N, R.6 E, section 2 (85WA91, 86WA53; USGS 3116, 2671, 5596). pp. 68, 81

AL-WI-9 Prairie Creek; Clayton Fm. (USGS 264). pp. 53,61, 68, 81, 83

AL-WI-12 Dales Branch, near Oak Hill. p. 53

AL-WI-13 2 mi W of Oak Hill. p. 53

AL-WI-16 "Black Bluff" beds, surface of prairies at Graveyard Hill, 3 mi W of Oak Hill Post Office; Clayton Fm. (USGS 3102 ?). p. 68

AL-WI-18 Lower Peachtree Ferry, Alabama River. pp. 83, 86

18b Lower Peachtree Ferry, "2nd fossil horizon, 60 ft. from top, 80 ft. from bottom of bluff" (Bowles, 1939, p. 299) (USGS 5602). p. 63

18c descent to Lower Peachtree Ferry; Tuscahoma Fm. (Cooke 1926, p.264) (USGS 10779) (= AL-WI-34). p. 63

AL-WI-21 Black Creek branch of Prairie Creek (USGS 283). pp. 68, 81

AL-WI-24 downgrade of Hwy. 21 toward creek, just north of jct. with Hwy. 28; type locality of Pine Barren Mbr.,MacBryde Mbr., Clayton Fm. (Toulmin, 1977, Loc. Awi-3; 85WA78) p. 68

AL-WI-25 outcrop on east side of road, approx. 2.0 miles north of jct of Hwy 41 and 10 at Camden; Lower Mbr., Porters Creek Fm. (Toulmin, 1977, Loc. Awi-27; 85WA79). p. 68

AL-WI-36 Clayton Fm. (USGS 281). pp. 68, 81

AL-WI-37 Clayton Fm. (USGS 284). pp. 68, 81

AL-WI-38 top of hill 0.8 mi W of J Lee Long Bridge in ditch and field near jct Ala Hwy 10 and 28 sec 7 T 13 N, R 7 E; Clayton Fm. (LaMoreaux and Toulmin, 1959, p.54) (Toulmin (1977) loc. 5). p. 68

AL-WI-39 Clayton Fm. (Toulmin (1977) loc. 31). p. 68

AL-WI-40 Clayton Fm. (Toulmin (1977) loc. 34). p. 68

AL-WI-41 Clayton Fm. (Toulmin (1977) loc. 37). p. 68

AL-WI-42 Porters Creek Fm. (Lower Member) (Toulmin (1977) loc. 8). p. 68, 81

AL-WI-43 Porters Creek Fm. (Lower Member) (Toulmin (1977) loc. 10). pp. 68, 81

AL-WI-44 Porters Creek Fm. (Lower Member) (Toulmin (1977) loc. 26). pp. 68, 81

AL-WI-45 Porters Creek Fm. (Matthews Landing Mbr.) (Toulmin (1977) loc. 11). pp. 68, 81

AL-WI-46 Porters Creek Fm. (Matthews Landing Mbr.) (Toulmin (1977) loc. 12). pp. 68, 81

AL-WI-47 Porters Creek Fm. (Matthews Landing Mbr.) (Toulmin (1977) loc. 13). pp. 68, 81

AL-WI-48 Porters Creek Fm. (Matthews Landing Mbr.) (Toulmin (1977) loc. 14). pp. 68, 81

AL-WI-49 Naheola Fm. (Coal Bluff Marl Mbr.) (Toulmin (1977) loc. 16). pp. 68

AL-WI-50 Clayton Fm. (Toulmin (1977) loc. 3). p. 81
AL-WI-51 Camden—Oak Hill Hwy [Hwy 10] road cut 9.9 mi E of Camden NE ¼ sec 10 T 11 N, R 9 E, at school near Rosebud Porters Creek Fm. (Lower Mbr.) (Toulmin (1977) loc. 9; 85WA80; Siesser, 1983, loc.A15). p. 81
AL-WI-52 Porters Creek Fm. (Lower Mbr.) (Toulmin (1977) loc. 35). p. 81
AL-WI-53 Naheola Fm. (Coal Bluff Marl Mbr.) (Toulmin (1977) loc. 20). pp. 53, 81
AL-WI-54 Naheola Fm. (Coal Bluff Marl Mbr.) (Toulmin (1977) loc. 25). p. 53
AL-WI-55 "new hwy to Camden, 9.7 mi W of Pineapple"; Nanafalia Fm. (USGS 10766). pp. 63, 86
AL-WI-57 Toulmin (1977) loc. 23. p. 63
AL-WI-58 Toulmin (1977) loc. 19. p. 63
AL-WI-59 "state Hwy 96, 10.3 mi NE of Kimbrough" (Stenzel and Turner, 1942, card 46) p. 53

ARKANSAS

Bradley County

AR-BR-1 well ~ 30 yds NW of Lee Hammaker's house, middle of sec. 8, T 12 S, R 9 W, approx. 18 mi w of Rison (USGS 2404). pp. 47, 49

Cleveland County

AR-CL-1 Vince Ferry, Saline River (PRI Loc. 897) 1b ¾ mi above Vince Bluff (USGS 2403). pp. 47, 49
AR-CL-4 well at Rison, NE ¼, sec 1, T 9 S, R 11 W (USGS 2231). pp. 47, 49 4b well at Rison, SE ¼, SW ¼, sec 1, T 9 S, R 11 W (USGS 2413). p. 49
AR-CL-7 well at the Orton place, Toledo (USGS 2410). p. 49
AR-CL-8½ mi N of Crossroads Church, 4.5 mi NW of Kingsland T 9 S, R 12 W, SW ¼ sec 22 (USGS 2420). p. 47

Drew County

AR-DR-1 Wadsworths well, Long Prairie. p.47

Jefferson County

AR-JF-1 White Bluff, left bank of Arkansas River ~ 3.5 mi E of Redfield, W ½, SE ¼, sec 19, T 2 S, R 10 W and W ½, NE ¼, NW ¼ sec 30, T 3 S, R 10 W [fossil bed covered by backwater from dam—1985] (USGS 2220). pp. 47, 49

Lonoke County

AR-LO-1 near Cabot (Harris, 1894, p.25-6). p. 61

Pulaski County

AR-PU-1 near Olsens switch, a few miles SW of Little Rock. p.68
AR-PU-4 Fourche Cr., near mouth of Crooked Creek, 8-9 mi SW of Little Rock (Stephenson and Crider, 1916, p.49). p. 61

St. Francis County

AR-SF-1 Hwy 70 over Crow Creek, approx. 3.0 mi. east of Forest City, approx. 0.5 mi. west of Madison, Madison 7.5 min. quad. R.3 E, T.5 N, section 25 (85WA56; PRI 1046; USGS 4157?). pp. 47, 49
AR-SF-2 upstream of RR bridge over Little Crow Creek, southwest of Madison, Madison 7.5 min. quad., T.5 N, R.3 E, section 36 (85WA57; USGS 4266?; PRI 1048). pp. 47, 49
AR-SF-4 Crowleys Ridge, Big Crow Creek (USGS 4156; PRI 894). pp. 47, 49

White County

AR-WH-1 Bradford (Harris, 1894, p. 25; Stephenson and Crider, 1916, p.51). p. 61
AR-WH-2 cut of St. Louis, Iron Mountain and Southern RR , ¼ mi S of Grandglaise (Stephenson and Crider, 1916, p.52). p. 61

FLORIDA

Citrus County

FL-CI-1 Large quarry around 5 mi.SE of Crystal River. (MacNeil, 1946.) p. 74
FL-CI-2 Suwannee River at Ellaville. (MacNeil, 1946.) p. 74

Leon County

FL-LE-1 "Road metal pit 2.9 mi S of the northern limits of the town of Gulf Hammock, just SW of state road 55." SW ¼ Sec. 34, T. 14 S, R. 16 E. p. 72
FL-LE-2 "About ⅛ mile below the Florida Power Corporation Plant at Inglis, Florida, on the right bank of the Withlacoochee River." SE ¼ NW ¼ Sec 3, T17S, R16E. p. 72.

Marion County

FL-MA-1 Martin Station, old railroad station, 10 mi N of Ocala, at junction of Hwy 441 and Martin-Anthony road. p. 74

GEORGIA

Bibb County

GA-BI-1 Brown's Mountain, near Bond's Store, 9 mi S of Macon (USGS 7696?). p. 69

Burke County

GA-BU-1 5.0 mi W of Waynesboro on Hwy. 24, E side of bridge over Rocky Creek (86WA03; USGS 3935?). p. 47
GA-BU-3 Sloan's Scarp, McBean Creek, between McBean Station and Savannah River, on Burke-Richmond Co. line (Veatch and Stephenson, 1911, p. 239) (USGS 5296). pp. 54, 69, 77
GA-BU-7 "McBean Creek, on land on Henry Byn" (Bowles, 1939, p. 287) (USGS 3288). p. 54
GA-BU-8 4.5 W of Hancock Landing, Savannah River (Veatch and Stephenson, 1911). p. 69
GA-BU-9 spring on Percy Boyd farm, 3.5 mi SW of Shell Bluff Post Office (Veatch and Stephenson, 1911). p. 69
GA-BU-10 "Dukes Bridge"—4 mi E of gouge on Waynesboro Rd. ("Barnwell"—ANSP collection). p. 69

Clay County

GA-CL-2 left bank of Chattahoochee River at approx. mi 71.3 above confluence with Flint River; Nanafalia Fm. (Bed 16, Toulmin and Lamoreaux, 1963) (86WA27). p. 63
GA-CL-3 right bank of Chattahoochee River, near Morris Landing, approx. 7 mi above Ft. Gaines; "collected at waters edge during a low level of the river" (Bowles, 1939, p.298) (USGS 5478). p. 61
GA-CL-4 old road, approx. 2 mi E of Days Crossroads, ¼–½ mi W of Fairview School, 9 mi N of Ft. Gaines; Tuscahoma Fm. (USGS 12018). p. 86
GA-CL-6 exposure on east bank of Chattahoochee R. at mile 80.5 (above confluence with Flint R.); Clayton Fm. (bed 8 of Toulmin and LaMoreaux, 1963) (Toulmin, 1977 loc. Gcl2). pp. 61, 91
GA-CL-7 just above mouth of Sandy Creek, Chattahoochee R. (ANSP collection). p. 63

Glascock County

GA-GL-1 English Plantation, 1.5 mi N of Gibson (Veatch and Stephenson, 1911, p.273). p. 69
GA-GL-2 "ss ledges at base of Barnwell near Rocky Comfort Creek"—Cooke, 1943, p.63. p. 49

Henry County

GA-HE-1 Chattahoochee River, Franklin Landing boat ramp; Nanafalia Fm. (Toulmin, 1977, Loc. AHe-1; 86WA26). p. 63

Houston County

GA-HO-1 Mossy Hill, 4.5 mi S of Perry (Veatch and Stephenson, 1911, p.258). p. 69
GA-HO-2 Perry-Elko public road, 4.5 mi S of Perry (Veatch and Stephenson, 1911, p.259). p. 69

Jefferson County

GA-JF-1 Old Town rd., E side of Boiling Spring Creek, 7.5 mi SE of Louisville (USGS 5247?, 7428?). p. 69

Jones County

GA-JO-1 cut on Ga RR 1 mi E of Roberts (Veatch and Stephenson, 1911, p.281); "McBean Fm.". pp. 46, 47, 49, 69

Macon County

GA-MA-1 Flint River at the county bridge, 1 mi NW of Montezuma; Clayton Fm. (USGS 3994). p. 61

Randolph County

GA-RA-1 approx. 1.8 mi S of Stewart-Randolph Co. line, approx. 9 mi N of Cuthbert; MacBryde limestone exposed as blocks and in bed of dirt road on west side of hwy. (Toulmin, 1977, Loc. GRa-1; 86WA21). p. 68
GA-RA-3 "Green's Branch", exposures along stream at small waterfall approx. 500 m W of Hwy. 266, 1 mi S of jct. with Co. Hwy. 15, access behind old farm barn, top of hill Bashi Fm. (GSA '80, stop 13, p.455) (86WA24). pp. 51, 73
GA-RA-4 old quarries 1 mi NW of Cuthbert (Veatch and Stephenson, 1911, p.266). p. 69

Schley County

GA-SL-1 5 mi W of Ellaville (USGS 12092). p. 81
GA-SL-2 Walls Crossing, 4-5 mi NW of Ellaville. p. 68
GA-SL-3 Lumkin Farm on Goldendale Creek, 6 mi SE of Ellaville (Veatch and Stephenson, 1911, p. 235). p. 61

Sumter County

GA-SU-1 50 foot bluff R side of Flint River, 16.5 mi E of Americus, near old Danville Ferry (Veatch and Stephenson, 1911, p.260). p. 69

Twiggs County

GA-TW-7 Gallemore Station (Veatch and Stephenson, 1911, p.256). p. 69

Washington County

GA-WA-4 2 mi S of Chalker (Veatch and Stephenson, 1911, p.276). p. 69
GA-WA-5 Little Keg Creek, 7 mi NNW of Sandersville (Cooke, 1943, p.55). p. 69

Webster County

GA-WE-1 Lime Spring, Cole property, 2 mi SE of Preston. p. 81

Wilkinson County

GA-WI-1 "farm of JW Huckabee, 1.5 mi N of Lewiston" (Veatch and Stephenson, 1911, p.278). p. 69

LOUISIANA

Bienville Parish

LA-BI-1 Holstons Well, 5 mi SE of Gibbsland (USGS 2033). pp. 51, 65
LA-BI-2 Mt. Lebanon (USGS 2911). pp. 51, 65
LA-BI-3 well at Rabun's place, sec 19 T 17 R 5 W (USGS 2037). p. 51
LA-BI-4 sec 17 T 18 R 5 W (USGS 2034). p. 65
LA-BI-5 bluff on Hammetts Branch, sec 30, T 18 R 5 W (USGS 2035). p. 65
LA-BI-6 well #1, sec 17 T 18 R 6 W (USGS 2045). p. 65
LA-BI-7 Hammetts Branch, 2 mi E of Mt. Lebanon (USGS 2400). p. 65
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Caldwell Parish

LA-CL-1 Gibson Landing, Ouachita River
1b,1d 1 mi above landing. p. 46
1c at landing. p. 46
1e ½ mi below landing. p.46
1g ¾ mi below landing. p.46
1h 1 mi below landing (PRI loc. P8). p. 46
LA-CL-2 Bunker Hill Bluff and Landing, right bank of Ouachita River at bend, Columbia 15 min. quad., R.5 E, T.13 N, section 19 (85WA60, 86WA75). p. 46
LA-CL-3 Grandview Bluff, Ouachita River . p. 46
LA-CL-6 Wyant Bluff (PRI loc. P2). p. 47

Catahoula Parish

LA-CA-1 Danville Landing, right bank Ouchita River at Catahoula-Caldwell Parish line, Harrisonburg 15 min. quad., T.11 N, R.5 E, section 15, T.10 N, R.5 E, section 22 (85WA52). p. 49
LA-CA-2 Carter Landing, Ouachita River. p. 49

Claiborne Parish

LA-CB-1 Pittmans Mill, SW ¼, SE ¼ sec 19 T 19 R 7 W (USGS 2038). p. 51
LA-CB-2 secs 1,2,11,12, T 19 N, R 6 W (USGS 10794). p. 65

Franklin Parish

LA-FR-1 well at Winnsboro (USGS 10456). p. 46

Grant Parish

LA-GR-1 (Creole Bluff) Montgomery Landing, bluffs below cemetery, E side of Red River, Montgomery 15 min. quad, R.5 W, T.8 N, sec 20 (PRI locs. 883,10,15; 85WA49, 86WA76). pp. 46, 47, 49, 50, 75
1a Montgomery Landing. p. 46
1d ½ mi below ferry (PRI loc. 883) . p. 47

Jackson Parish

LA-JA-2 "from gullies north of old Quitman-Liberty Hill Road on Mrs. JM Turners place west of Madden Creek, sec 15, T 16 N, R 3 W, 3.6 mi W of Quitman RR xing" (TBEG loc. La-7) (Stenzel and Turner, 1940). p. 51

La Salle Parish

LA-LS-1 "Urania well no. 1, drilled by the Simms Oil Co. at Urania" (Bowles, 1939, p. 307) (USGS 8931). p. 46

Natchitoches Parish

LA-NA-5 Road cut along local road in center of NE ¼ Ne ¼ sec 19, T 9 N, R 8 W; Pendleton Fm. (Le Blanc (1942) loc. 59). p. 63
LA-NA-6 Road cut in NW ¼ SE ¼ sec 33, T 10 N, R 10 W, along dirt road leading west from L. Hwy. 404; Midway Group (Le Blanc (1942) loc. 8). pp. 81, 84
LA-NA-12 RR cut 75 yds E of depot at Marthaville; Marthaville Fm. (LeBlanc (1942) loc. 21) p. 63
LA-NA-14 about 50 yds N of La Hwy 1 in Roe's field, NW ¼, NE ¼ SW ¼ sec 26, T 9 N, R 10 W; Marthaville Fm. (LeBlanc (1942) loc 16). p. 63
LA-NA-15 road cut along local road, SW ¼ NW ¼ SE ¼ sec 24 T 9 N, R 10 W; Marthaville Fm. (LeBlanc, 1942, loc. 15). p. 63
LA-NA-16 Pendleton Fm. (Le Blanc, 1942, Loc.55). pp 63, 86
LA-NA-17 Pendleton Fm. (Le Blanc, 1942, Loc. 56). p. 63

Rapides Parish

LA-RA-1 well 2 mi NW of Boyce (Bowles, 1939, p. 277) (USGS 7743). p. 47
LA-RA-2 well of Cotile Oil and Gas Co., near Boyce (Bowles, 1939, p. 277) (USGS 7944). p. 47
LA-RA-3 Boyce Oil Co. Well, 6 mi SW of Boyce (1535-2766') (USGS 7247). p. 75

Sabine Parish

LA-SA-9 Undifferentiated Midway Group (Le Blanc (1942) loc. 1). p. 84
LA-SA-19 Marthaville Fm. (Le Blanc, 1942, Loc.37). p. 83
LA-SA-20 Pendleton Fm. (Wassem and Wilbert (1943) loc. 4). pp. 63, 83
LA-SA-21 Pendleton Fm. (Wassem and Wilbert (1943) loc. 5). pp. 63, 83, 86
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Winn Parish

LA-WI-1 St. Maurice, Saline Bayou (USGS 2005, 2916, 4272). pp. 46, 51, 69, 78
LA-WI-2 c. 10 mi NW of Winnfield (USGS 2919). p. 51

MARYLAND

Anne Arundel County

MD-AA-5 South River, 2.5 mi from Annapolis (USGS 3934) (=? MD-AA-3). pp. 55, 85

Charles County

MD-CH-2 Popes Creek. p. 65
MD-CH-7 Glymont, bluff on E side of Potomac River, 0.5 mi N of Potomac Heights. p. 55

Prince Georges County

MD-PG-3 Upper Marlboro. p. 55
MD-PG-5 Piscataway (USGS 13451). pp. 55, 85
MD-PG-7 E bank of creek 100 yds NNW of reservation parking area A-A at Fort Washington Park, ¾ mi NNE of Fort Washington (=? USGS 2370) p. 85
MD-PG-10 ravine, 1 mi E of Fort Washington (USGS 2029). pp. 55, 85
MD-PG-12 south bluff of Southwest Branch, just west of Capital Beltway and jct with Central Ave. (no longer exposed); Brightseat Fm. (Govoni (1983) loc. A). pp. 64, 90
MD-PG-13 banks and stream bed of small tributary to Cattail Branch, just south of Sheriff Road and east of Paca School and west of jct of Brightseat Rd with Sheriff Rd. (no longer exposed); Brightseat Fm. (Govoni (1983) loc. B). pp. 64, 90
MD-PG-14 banks of small tributary to Cabin Branch, just south of Central Ave (Md Hwy 214) just east of jct with Addison Rd.; Brightseat Formation (Govoni (1983) loc. C). pp. 64, 90

MISSISSIPPI

Clarke County

MS-CL-1 cuts on both sides of the Southern Railroad north of Wattubbee, T.3 N, R.14 E, sec 3 Archusa Marl Mbr, Cook Mtn Fm. (MGS Loc. 61,62; 85WA29,30) [these localities are probably at or near locality usually called "Wattubbee" or "Wattubbee Hills" by earlier authors—fide Dockery, 1980:14; USGS 338, 2616, 3092, 6479). pp. 51, 54, 69, 77, 79
MS-CL-2 in wash of Rose Hill Road, 8 mi W of Enterprise (USGS 2621; PRI 729). pp. 51, 54, 77
MS-CL-3 high bank of Garland Creek, about 1 mi. upstream along right fork, T.1 N, R.16 E, sec 28 (MGS Loc. 9; 85WA70; USGS 6471) [Garland Creek loc. of authors = USGS 330, 2630, 6471]. pp. 46, 47, 75
MS-CL-5 2-3 mi E of Shubuta. p. 54
MS-CL-7 McLeod's mill, Suwanlovey Cr., 6 mi W of Desoto sta. on RR (USGS 14220). p. 54
MS-CL-15 left bank of Chickasawhay River, at bend just below old hunting lodge, T.1 N,R.16 E, section 30 (MGS Loc. 16; 85WA72). pp. 47, 75
MS-CL-16 "wash of Old Enterprise road, at residence of Mr. J.Harrison Johnson, 8 mi S of Hickory and 12 mi NW of Enterprise" (Bowles, 1939, p. 279) (USGS 2622). pp. 51, 54, 69, 77
MS-CL-17 "in a washed off place in Mr. J.H.Johnson's farm, south of the creek and about 9 ½ miles south of Hickory" (Bowles, 1939, p. 279) (USGS 2623). pp. 51, 54, 69, 77
MS-CL-18 S bank of Chickasawhay River at bridge on Hwy. 45, 1 mi S of Quitman (USGS 14218). pp. 47, 54
MS-CL-19 bluff on old bridge site on SW bank of Chickasawhay River, De Soto (USGS 14229; MS-CL-4?). p. 54

Hinds County

MS-HN-1 Jackson. p.47
1b "Greens marl bed" (USGS 54, 58). pp. 46, 75
1c "Jackson marl bed" (USGS 64, 3665, 13398). p. 46
1d "south of pump house" (USGS 734). p. 46
1e "Bailey's Marl Bed" (USGS 59). p. 75
MS-HN-2 Dry Creek, Jackson. p. 46
MS-HN-3 Town Creek. pp. 46, 75, 78
MS-HN-4 Moody's Branch (USGS 60, 63, 3735, 3746, 6462, 10377). pp. 46, 47, 75 4b Moody's Branch, first bluff below first bridge, east of the Institute for the Blind (USGS 4250). p. 46
MS-HN-6 Riverside Park, Jackson, ravine behind old Riverside swimming pool, T.6 N, R.1 E,sect 36; Moody's Branch Fm. (MGS Loc. 2; 85WA24). pp. 46, 75, 78

Lauderdale County

MS-LA-3 McKays Marl Bed, Souwashee Creek, 2 mi S of Meridian; Bashi Fm. (USGS 2105) p. 73
MS-LA-4 "cut on Memphis and Meridian RR, 300 yards south of Seymours Hill, 1 ½ miles south of Meridian" (Bowles, 1939, p. 303); Bashi Fm. (USGS 7267, 7734, 10055). p. 73

Newton County

MS-NE-1 "Indian mound railroad cut on the side of Pottoxchitto

swamp, 4 ½ miles east of Newton" (Bowles, 1939, p. 279) (PRI loc. 726; USGS 2620, 14058; MGS 67). pp. 51, 54, 69, 77,
MS-NE-2 Hickory. p 51, 69, 79
MS-NE-3 2 mi NE of Newton on Rt 15 (PRI loc. 1803). p. 69
MS-NE-7 jct. of I-20 and Hwy.15, outcrop in grass behind gas station, southwest corner of intersection; Cook Mountain Fm. (85WA41; MGS 65). p. 69
MS-NE-9 "in wash of road from Newton to Decatur, about 3 miles northeast of Newton, in hill going down to Pottoxchitto Creek" (Bowles, 1939, p. 279) (USGS 2618). p. 77
MS-NE-10 "in wash of old Enterprise road, going down the hill to the Pottoxchitto swamp, 2 miles southeast of Hickory" (Bowles, 1939, p. 279) (USGS 2624; MS-NE-5?). pp. 51, 54, 69, 78
MS-NE-11 "in wash of the old General Jackson road from Nashville, Tennessee to New Orleans, 1 mile south of Hickory" (Bowles, 1939, p. 279) (USGS 2625). pp. 51, 77

Tippah County

MS-TI-8 type section of Owl Creek Fm. (Cretaceous), Ripley 7.5 min. quad., approx. 2.75 mi NE of Ripley; Clayton Limestone exposed upstream from best Owl Creek exposures (86WA69; USGS 6497?). p. 80
MS-TI-9 ravine just N of Booneville Rd., 3 mi NE of Ripley (USGS 5586). p. 80
MS-TI-10 bluff on small stream approx. 1.5 mi S of Ripley (USGS 6496). p. 80

Yazoo County

MS-YZ-1 Sims Siding, 8 mi N of Yazoo City, "roadside on hill at Sims Station, Yazoo & Miss. RR 10 mi N of Yazoo City, 2 mi S of Eden" (USGS 7674). pp. 49, 78
MS-YZ-2 Tcheva Creek, just upstream from Hwy. bridge, T.13 N, R.1 E, section 32 Moody's Branch Fm. (MGS Loc. 11; 85WA65). pp. 49, 50, 75
MS-YZ-4 Locust Grove Plantation, 1.5 mi S of Sartartia (Bowles, 1939, p. 277) (USGS 7393). p. 47
MS-YZ-5 Miss Lite Clay Pit at Cynthia, T.7 N, R.1 W, sec 25; Yazoo Clay (MGS Loc. 15; 85WA64; =MS-HN-7). p. 47
MS-YZ-6 near head of ravine, ¾ mi SE of Free Run on line betw se ¼ sec 26 and sw ¼ sec 25 T 13 N, R 1 W, 10 mi NE of Yazoo City (USGS 10118). p. 78

SOUTH CAROLINA

Aiken County

SC-AI-1 Hixon Branch, Tinkers Creek, public rd. 200 ft. E of bridge, 12.5 mi W of Williston (USGS 4603). p. 78

Berkeley County

SC-BE-3 Wilson's Landing, R bank of Santee River just below Santee dam; Black Mingo Fm. (only visible at very low water, 1985) (86WA115). pp. 55, 88

Clarendon County

SC-CL-2 Kingstree Rd. E of Deep Cr., 5 mi E of Manning; Black Mingo Fm. (USGS 10403) p. 55

Lexington County

SC-LE-1 "property of Eugene Senn, north of Kennerly road, Lexinton-Calhoun county line, 18 mi north of house, 7 miles east of Swansea" (Bowles, 1939, p. 287) (USGS 7731) . pp. 54, 78
SC-LE-2 "south of old Bethel Church and east of Lexington-Orangeburg road, about 2 miles southeast of Edmund" (Bowles, 1939, p. 287) (USGS 7732). p. 54

Orangeburg County

SC-OR-1 3 mi WNW of Orangeburg. pp 77, 79
SC-OR-3 6 mi WNW of Orangeburg. p. 79
SC-OR-5 Old Columbia Rd., south of Early Branch, 5 mi N of Orangeburg (USGS 7722). p. 54
SC-OR-6 Poosers Hill, 5.1 mi N of Orangeburg (USGS 4580). pp. 54, 69, 80
SC-OR-7 Caw-Caw swamp, 2 mi W of Orangeburg (USGS 2009). pp.54, 69, 79
SC-OR-10 Stroman's Mill, 5 mi SE of Springfield (USGS 7816). p. 54
SC-OR-11 "at old brickyard in Orangeburg" (Bowles, 1939, p. 287) (USGS 2021). p. 54

Sumter County

SC-SU-2 approx. 3.5 mi W of Pinewood; Black Mingo Fm. (USGS 10401). p. 55

Williamsburg County

SC-WI-1 roadside, 1.1 mi S of Salters. p. 78

TENNESSEE

Hardeman County

TTN-HA-7a 1.5 mi E of Middleton, 200 ft W of milepost 481 (USGS 6091). p. 80
TN-HA-7b 200 ft. E of milepost 481 (USGS 6495). p. 80
TN-HA-12 McDonald's Mill, 4 mi SW of Middleton (USGS 2148). p. 61

TEXAS

Anderson County

TX-AN-2 1.5 mi SE of Palestine on the Boston Rd. (USGS 10852). p. 51
TX-AN-3 .5 mi E of Robinson on Centerville Rd. (USGS 13266). p. 51

Atascosa County

TX-AT-2 1 mi E of Jourdanton on the Pleasanton Rd. (USGS 13231). p. 50
TX-AT-3 ¼ mi NW of Jourdanton (USGS 8870). p. 50

Bastrop County

TX-BA-1 Colorado River, ~ 4 mi below Webberville; Kincaid Fm. (USGS 5280) 1c 5 mi below Webberville. p. 53
TX-BA-2 Colorado River at mouth of Dry Creek 2b ½ mi above Dry Creek (USGS 10526). p. 53
TX-BA-3 bluff on right bank of Colorado River, approx. 200 m downstream from Hwy 71 bridge at Smithville; Viesca Mbr., Weches Fm. (TBEG loc. 11-T-2; USGS 6088, 10386) [outcrop overgrown and inaccessible 1985, 1986]. p. 78
TX-BA-15 1.5-2 mi below Travis-Bastrop Co. line; Wills Point Fm. (USGS 11890, 11913, 12113). p. 53
TX-BA-30 Cedar Creek approx 4 mi SE of Williams Store (USGS 11909). p. 68
TX-BA-31 roadside gully ½ mi E of Williams store, Austin Quad. (USGS 11911). p. 68
TX-BA-32 approx. 3 mi SE of Williams store (Gardner, 1935) (USGS 11910). p. 68

Brazos County

TX-BR-1 Little Brazos River, upstream from Hwy. 21 bridge; Wheelock Mbr., Cook Mountain Fm. (85WA07; USGS 14210). p. 50

Burleson County

TX-BU-1 Stone City Bluff ("Moseley's Ferry), south bank of Brazos River just downstream of Hwy. 21 bridge, ~ 11 mi W of Bryan; Stone City Beds (85WA06; TBEG loc. 26-T-1; PRI loc. 723; USGS 5473). pp. 50, 73
TX-BU-2 [see TX-RO-10]. p. 73

Caldwell County

TX-CA-1 5.5 mi N of Lockhart; Kincaid Fm. (= E.A.Moser farm approx ½ mi NW of Sims' oil derrick, USGS 11707) (= TX-CA-3). p. 68

Falls County

TX-FL-7 roadside gully, ¼ mi NW of Stranger School (USGS 11932). p. 68

Houston County

TX-HO-2 left bank Trinity River, just upstream from old Alabama Ferry; access via FM 132 SW of Porter Springs (TBEG loc. 113-T-9; 86WA78; USGS 10738, 10735, 10736). p. 79
TX-HO-13 "Jose Procela League, from water well dug at village gin in 1916, Percilla" (USGS 9257). p. 77

Hunt County

TX-HU-1 approx 14 mi SE of Greenville on Lone Oak pike approx. 50 yds from pike on E side of Cowleach fork just as road climbs hill on NE side on pike (USGS 10264). p. 68

Kaufman County

TX-KA-1 Water Hill, 5 mi NE of Kemp; Kincaid Fm. (USGS 11665?). p. 68
TX-KA-4 4 mi NE of Kemp (USGS 2440). p. 68
TX-KA-5 old Flat Rock Quarry (now flooded), approx. 5 mi S of Ola (85WA20). p. 66

La Salle County

TX-LA-1 south side Hwy. 97, 2.8 mi. east of jct. with Hwy. 81 at Cotulla (USGS 14296; 86WA116). p. 72
TX-LA-2 2 mi SW of Shelton Ranch House, 2.5 mi SW of Millet (USGS 14298). p. 72
TX-LA-3 shingle below Brinkley Ranch house, 4 mi NE of Cotulla (USGS 14293). p. 72
TX-LA-4 1 mi SW of windmill near Altita Ranch house, 3.5 mi NE of Cotulla (USGS 14297). p. 72
TX-LA-5 ½ mi SE of Rockwood on Cotulla-LaMotta Ranch Rd. (USGS 14295). p. 72

Lee County

TX-LE-11 between Orells and Price's Crossings, Elm Creek. p. 51
TX-LE-12 "2 mile creek, first ford above 2 mile Negro Church", 3-4 mi S of Middleton (USGS 14213). p. 79

Leon County

TX-LO-12 ditch on N side of Concord-Centerville Rd, o.6 mi SE of Robbins crossroad in S corner of JMPowell 100 acre tract, S corner of RMTyus survey (Stenzel and Turner). p. 51
TX-LO-13 bluff on Navasota River, near old iron bridge on E.C.Watson 800 acres, J.M.Viesca survey, SW part of county (Renick and Stenzel, 1931, loc. 8). p. 51

Limestone County

TX-LI-2a 2.5 mi NW of Groesbeck p. 82
TX-LI-3 limestone quarry of D.P.Frost Construction Co., south side of Hwy. 84, west of jct. of Hwy. 84 and Hwy. 14 in Mexia; Tehuacana Limestone (85WA19). p. 67

Maverick County

TX-MV-1 Bibora Tank, 18 mi S of Eagle Pass (USGS 6583, 11753). p. 82
TX-MV-4a land of Indio Cattle Co., 1 ¾ mi below White Bluff, ~ 4 ½ mi SW of Jacal Ranch house
4b 3.5–4 mi SW of house, Las Islas crossing rd. (USGS 11763). p. 82
TX-MV-6 Indio Wells, 29 mi S of Eagle Pass. p. 82

Nacogdoches County

TX-NA-7 road cut 4.8 miles east of Melrose (85WA55). p. 48
TX-NA-8 road side ditch on road from Chireno to St. Hwy 21 North of town (Stenzel and Turner). p. 48

Robertson County

TX-RO-6 Dunn's Ranch. p. 51
TX-RO-11 Montgomery's well, ½ mile E of Wheelock (USGS 2048). p. 50
TX-RO-12 Taylors well. 5 mi SE of Franklin, 6 mi NW of Wheelock (USGS 2050). pp. 51, 78

Sabine County

TX-SA-2b ½ mi below Robinson's Ferry, center sec 6, T 3 N, R 12 W (USGS 10516). pp. 47, 50
TX-SA-3 Sabine River (otcp. 22 of Veatch, 1902). p. 79
TX-SA-4 bluff ~ ¼ mi below Sabinetown ferry landing, ~ ¼ mi up from bridge (LeBlanc, 1942, loc. 40). pp. 83, 86
TX-SA-5 Pendleton, ¼ mi down from bridge over Sabine R. on LA Hwy 6. p. 63 5c ¼ mi above Pendleton Ferry. p. 63
TX-SA-19 (Le Blanc, 1942, loc. 51). pp. 63, 83

Starr County

TX-ST-1 Alta Vista Ranch, 5.8 mi W, 35° N of Rio Grande City (USGS 13799). p. 47

Zapata County

TX-ZA-2 1.1 mi NE of benchmark 400, Zapata-Hebbronville Rd. (USGS 14290). p. 72
TX-ZA-3 scarp on S side of Arroyo El Tigre above and below bridge on Laredo-Roma Hwy. (USGS 141165, 66, 67, 68). p. 72
TX-ZA-4 hillside ½ mi ENE of Fordyce Ranch house (USGS 14291). p. 72
TX-ZA-5 first bench above Rio Grande above Rio Grande south of Ramireno Ford (USGS 14292). p. 72

VIRGINIA

Hanover County

VA-HA-2 right bank of Pamunkey River, 0.5 mi. E of Wickham railroad crossing; Piscataway Mbr., Aquia Fm. (86WA106; USGS 26337). pp. 55, 65, 85
VA-HA-3 right bank of Pamunkey River, small ravine 0.63 SE of mouth of Totopotomoy Creek; Woodstock Mbr., Nanjemoy Fm. (86WA107; USGS 26403). p.66
VA-HA-4 right bank of Pamunkey River, small ravine 3-400 m downstream from VA-HA-3; Piney Point Fm. over Woodstock Mbr., Nanjemoy Fm. (86WA108). p. 66

King George County

VA-KG-3 Woodstock. p. 65

VA-KG-5 Belvedere Beach, low bluff approx. 0.6 mi S of mouth of Potomac Creek. p. 88

Stafford County

VA-ST-2 "Aquia Creek". p. 85
VA-ST-4 high cliff on western shore of Potomac River between mouths of Aquia and Potomac Creeks; Aquia Fm. (86WA99) (=? USGS 2347). pp. 55, 85, 88
VA-ST-5 Stafford Courthouse (USGS 12934). pp. 55, 85
VA-ST-6 bluffs at mouth of Aquia Creek (USGS 2030, 13809, 13810). pp. 55, 85, 88

MEXICO

Nuevo Leon

MX-NL-3 1200 feet N and 1300 feet E of Rancho la Rosita, in arroyo, Zacate district. (USGS 13512.) pp. 47, 72
MX-NL-4 275 m from Rancho Paredila toward Ranch San Agustin. (USGS 13763) p. 86

Tamaulipas

MX-TA-1 15.9 km S of Cividad Camargo. (USGS 13504). pp. 47, 72
MX-TA-2 1 km N of Villa Neuva or Neuvo Camargo, Camargo Seder, La Mision. (USGS 13506). pp. 47, 72

RECENT LOCALITIES

R-1 NW of Samar Island, Philippines. 17 fms. (MCZM). p. 101
R-2 Manila Bay, Philippines. 20 fms. (MCZM). p. 101
R-3 Philippines. (MCZM 111526). p. 101
R-4 Philippines. (MCZM 224596). p. 101
R-5 Near Cavite, Manila Bay, Philippines. (MCZM). p. 101
R-6 Darwin, Northen Australia. (MCZM). p. 101
R-7 Manila Bay, Philippines. MCZM 43097, 141712). p. 101
R-8 East Point, near Darwin, Northern Australia. (MCZM). p. 101

PLATES

EXPLANATION OF PLATE 1

Figure Page

1–3. *Palmerella mortoni* ssp. ("*premortoni*" Govoni, 1983). 64

1. Scanning electron micrograph of apex. Unnumbered USNM specimen. Brightseat Fm., Locality MD-PG-12. ×85
2. Scanning electron micrograph of apex showing protoconch and initiation of spiral sculpture. Same specimen as Figure 1. ×200
3. Holotype unnumbered USNM specimen. Brightseat Fm., Locality MD-PG-12. Height = 39.9 mm.

4–6. *Palmerella mortoni mortoni* (Conrad). 54

4. Holotype ? ANSP 15508. Aquia Fm., Locality MD-PG-5 ? Height = 59.9 mm.
5. Scanning electron micrograph of apex. MCZIP 29320b. Aquia Fm., Locality VA-KG-5. ×26.
6. Scanning electron micrograph of apex showing protoconch and initiation of spiral sculpture. Same specimen as Figure 5. ×140.

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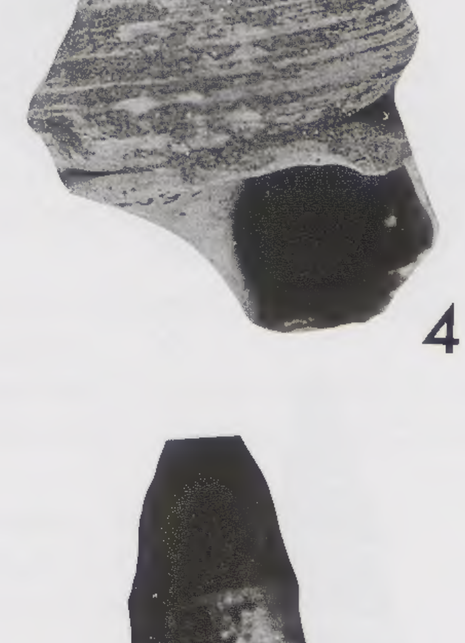

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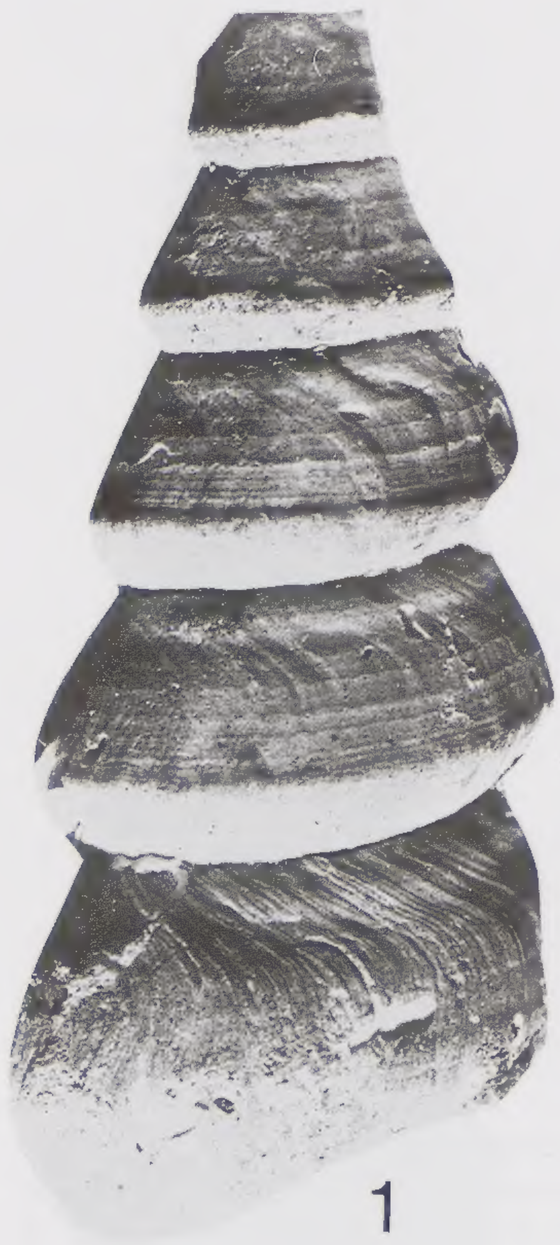

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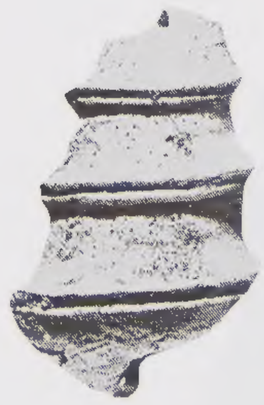

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EXPLANATION OF PLATE 2

Figure — Page

1,9. *Palmerella mortoni mediavia* (Bowles). 61

1. Latex cast of ANSP 11884. Clayton Fm. ?, Locality GA-CL-7. Height = 71.5 mm.
9. Holotype USNM 495146. Clayton Fm., Locality AL-WI-9. Height = 41.0 mm.

2–5. *Palmerella mortoni postmortoni* (Harris). 61

2,3. Unnumbered GSA specimens. Nanafalia Fm., Locality AL-DA-1. Heights, Figure 2 = 91.2 mm., Figure 3 = 31.9 mm. (From Toulmin, 1977, pl. 29, figs. 12,13). Note double carinae.
4. MCZIP 29308. Tuscahoma Fm., Bells Landing Marl Mbr., Locality AL-MO-3. Height = 74.2 mm.
5. MCZIP 29329a. Tuscahoma Fm., Bells Landing Marl Mbr., Locality AL-MO-3. Height = 51.2 mm. Note double carina.

6–8. *Palmerella mortoni mortoni* (Conrad). 54

6. MCZIP 29099. Aquia Fm., Locality VA-KG-6. Height = 104.4 mm.
7. MCZIP 29307. Aquia Fm., Locality VA-KG-6. Height = 110.0 mm.
8. USNM 497988. Black Mingo Group, Locality SC-SU-2. Height = 57.0 mm.

EXPLANATION OF PLATE 3

Figure — Page

1,2. *Palmerella lisbonensis* (Bowles). 53

1. Holotype USNM 498009. Lisbon Fm., Locality AL-MO-4d. Height = 39.5 mm. (From Stenzel and Turner, 1942)
2. MCZIP 29311. Lisbon Fm., Locality AL-CL-14. Height = 29.8 mm.

3–6. *Palmerella femina* (Stenzel). 51

3. Scanning electron micrograph of apex showing protoconch and initiation of spiral sculpture. MCZIP 29322a. Weches Fm., Locality TX-RO-5. ×110.
4. Scanning electron micrograph of apex. Same specimen as Figure 3. ×32.
5. MCZIP 29309. Weches Fm., Locality TX-RO-5. Height = 25.9 mm.
6. MCZIP 29320. Bashi Fm., Locality AL-CO-1. Height = 24.6.

7–9. *Palmerella chirena* (Stenzel and Turner). 47

7. Scanning electron micrograph of apex. MCZIP 29323. Weches Fm., Locality TX-NA-7. ×36.
8. Holotype TBEG 20960. Weches Fm., Locality TX-NA-8. Height = 19.5 mm.
9. Scanning electron micrograph of apex, showing protoconch and initiation of spiral sculpture. Same specimen as Figure 7. ×210

10–12. *Palmerella dutexata* (Harris). 50

10. Hypotype PRI 2912. Cook Mountain Fm. ?, Locality TX-RO-14. Height = 26 mm.
11. Scanning electron micrograph of apex. MCZIP 29324. Lisbon Fm., Locality AL-CL-14. ×35.
12. Scanning electron micrograph of apex showing protoconch and initiation of spiral sculpture. Same specimen as Figure 11. ×180

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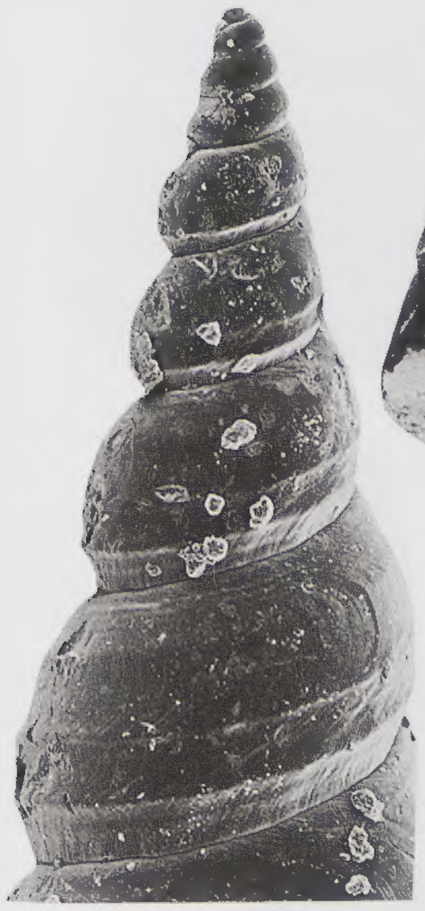

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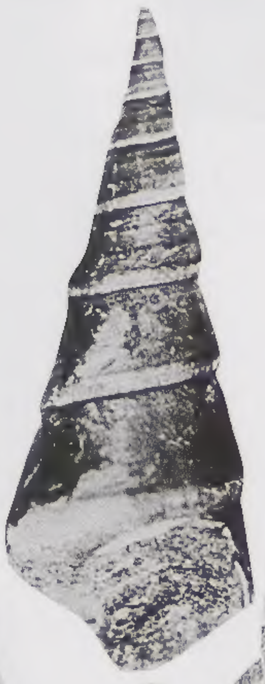

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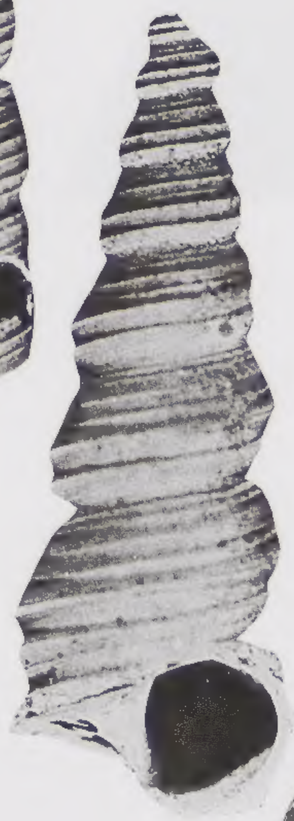

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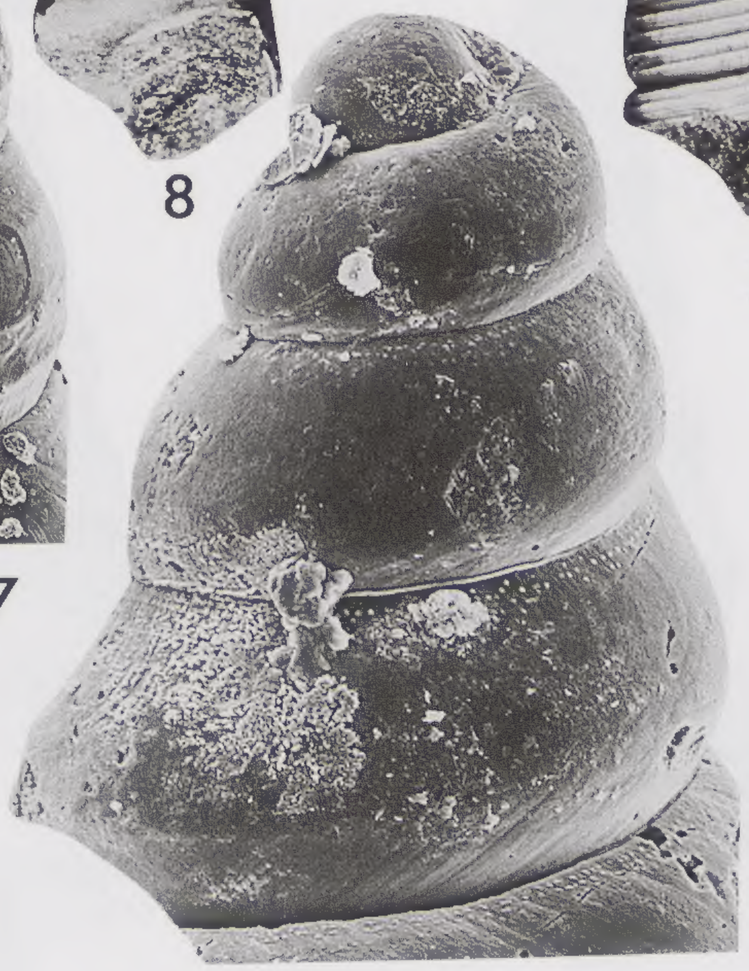

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EXPLANATION OF PLATE 4

Figure

1–5. *Palmerella creola* (Palmer). 49
1. Holotype PRI 4579. Moodys Branch Fm., Locality LA-GR-1. Height = 32.5 mm.
2. MCZIP 29315. Moodys Branch Fm., Locality LA-GR-1. Height = 24.5 mm.
3. Scanning electron micrograph showing protoconch and initiation of spiral sculpture. MCZIP 29325a. Moodys Branch Fm., Locality LA-GR-1. ×220.
4. Scanning electron micrograph. Same specimen as Figure 3. ×110.
5. Scanning electron micrograph of apex. MCZIP 29326a. Moodys Branch Fm., Locality LA-GR-1. ×21.

6,7. *Palmerella apita* (de Gregorio). 46
6. MCZIP 29290. Gosport Sand, Locality AL-CL-4. Height = 25.2 mm.
7. MCZIP 29347. Gosport Sand, Locality AL-CL-4. Height = 20.8 mm.

EXPLANATION OF PLATE 5

Figure — Page

1,2. *Palmerella clevelandia* (Harris). 48

1. Holotype USNM 498010. White Bluff Fm., Locality AR-JF-1. Height = 24.1 mm.
2. Scanning electron micrograph of broken apex showing early teleoconch sculpture. MCZIP 29327b. Moodys Branch Fm., Locality LA-GR-1. ×140

3–6. *Palmerella arenicola* (Conrad). 46

3. MCZIP 29314. Moodys Branch Fm., Locality MS-CL-3. Height = 32.3 mm.
4. Scanning electron micrograph of apex. MCZIP 29328. Moodys Branch Fm., Locality MS-CL-15. ×30
5. Scanning electron micrograph of broken apex showing initiation of spiral sculpture. Same specimen as Figure 4. ×180
6. MCZIP 29316. Yazoo Fm., Danville Landing Mbr., Locality LA-CA-1. Height = 34.2 mm.

7–9. *Palmerella alveata* (Conrad). 45

7. Lectotype ANSP 13213. Moodys Branch Fm., Locality MS-HN-4. Height = 48.1 mm.
8. Scanning electron micrograph of apex. MCZIP 29325b. Moodys Branch Fm., Locality LA-GR-1. ×32.
9. Scanning electron micrograph of apex showing protoconch and initiation of spiral sculpture. Same specimen as Figure 8. ×250.

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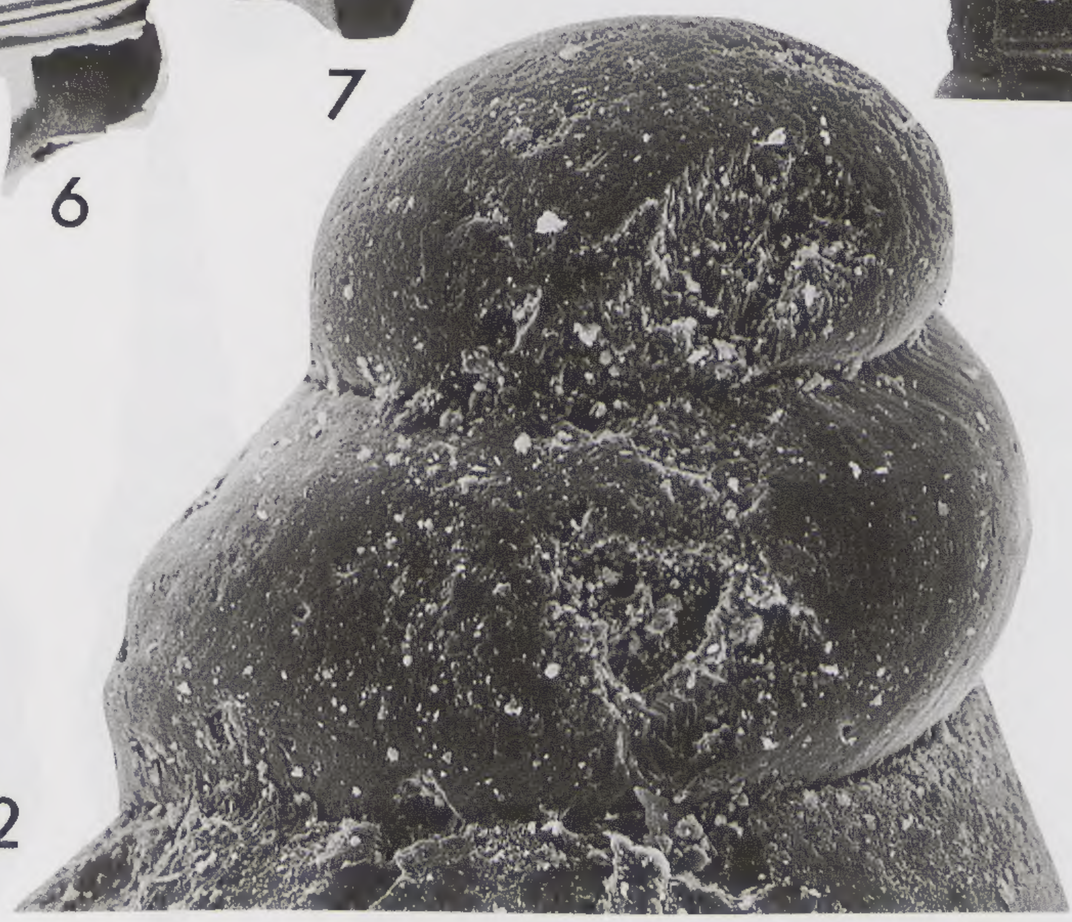

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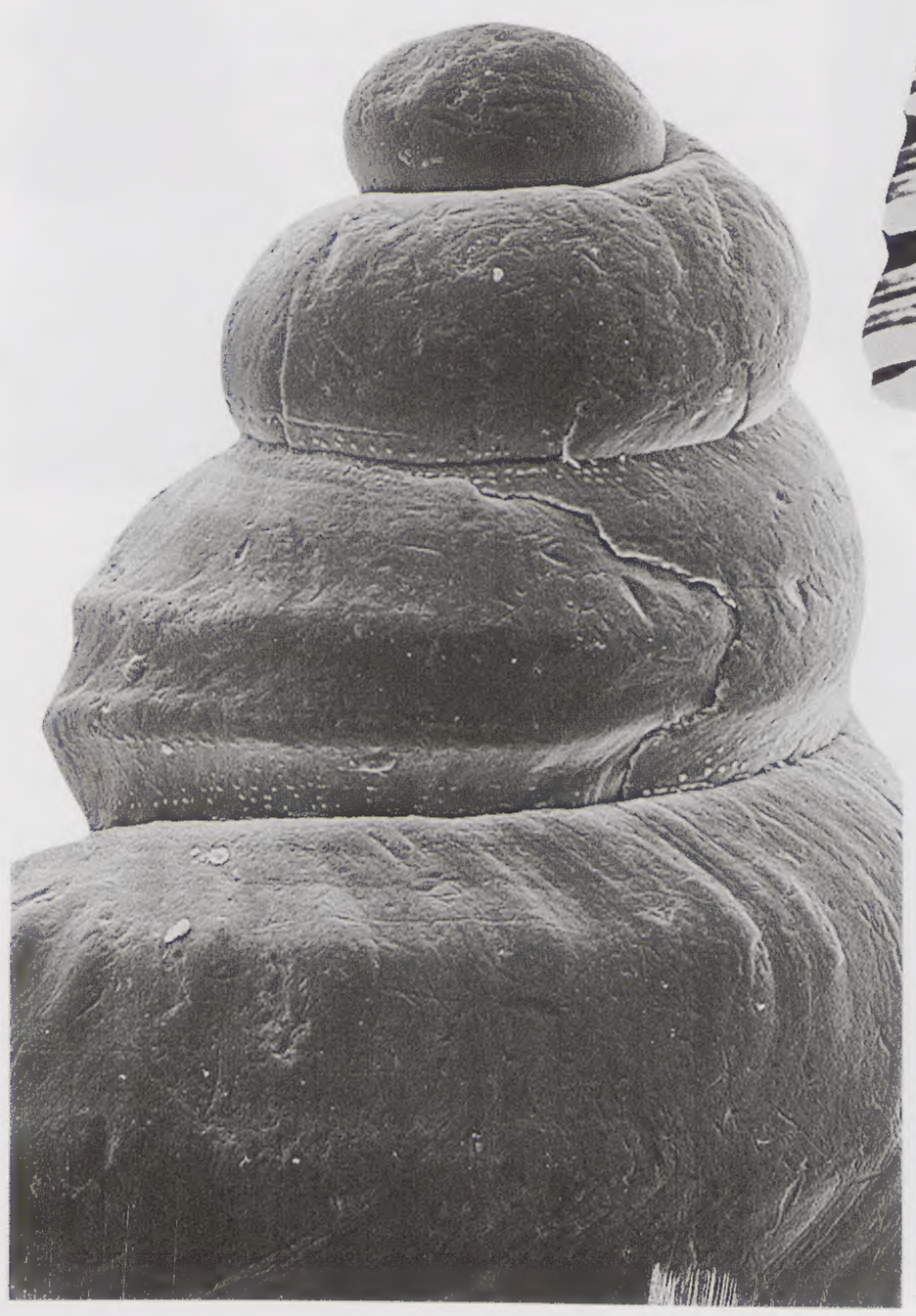
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EXPLANATION OF PLATE 6

Figure — Page

1–3. *Palmerella pleboides* (Vaughan). 65

1. Scanning electron micrograph of apex and early teleoconch whorls. USNM 138264. Cook Mountain Fm., Locality LA-BI-1. ×16.
2. Scanning electron micrograph of apex showing protoconch and initiation of spiral sculpture. Same specimen as Figure 1. ×230.
3. USNM 138264. Cook Mountain Fm., Locality LA-BI-1. Height = 17.3 mm.

4–6. *Palmerella dumblei* (Harris). 50

4. MCZIP 29317. Stone City Beds, Locality TX-BU-1. Height = 28.1 mm.
5. Scanning electron micrograph of apex. USNM specimen. USGS 1/742. Cook Mountain Formation ?, Locality TX-SA-2b. ×32
6. Scanning electron micrograph of apex, showing protoconch and initiation of spiral sculpture. USNM specimen. USGS 13231. Cook Mountain Fm.?, Locality TX-AT-2. ×190.

EXPLANATION OF PLATE 7

Figure — Page

1–3. *Haustator alabamiensis* (Whitfield). 67

1. Syntype FMNH-UC 24522. Porters Creek Fm., Matthews Landing Marl Mbr., Locality AL-WI-3. Height = 35.0 mm.
2. Scanning electron micrograph of apex and early teleoconch whorls. MCZIP 29343. Porters Creek Fm., Matthews Landing Marl Mbr., Locality AL-WI-3. ×15.
3. Scanning electron micrograph of damaged apex showing initiation of spiral sculpture. MCZIP 29344. Porters Creek Fm., Matthews Landing Member, Locality AL-WI-3. ×120.

4,5. *Haustator gilberti* (Bowles). 72

4. Holotype USNM 494993. Bashi Fm., Locality AL-CL-2. Height = 35.5 mm.
5. MCZIP 29345b. Bashi Fm., Locality AL-CO-1. ×150.

6–8. *Haustator tennesseensis* (Gabb). 79

6. USNM specimen. USGS 6495. Clayton Fm., Locality TN-HA-7b. Height = 23.2 mm.
7. USNM specimen. USGS 6495. Clayton Fm., Locality TN-HA-7b. Height = 22.8 mm.
8. Scanning electron micrograph of apex and early teleoconch whorls showing initiation of spiral sculpture. USNM specimen. USGS 6495. Clayton Fm., Locality TN-HA-7b. ×58.

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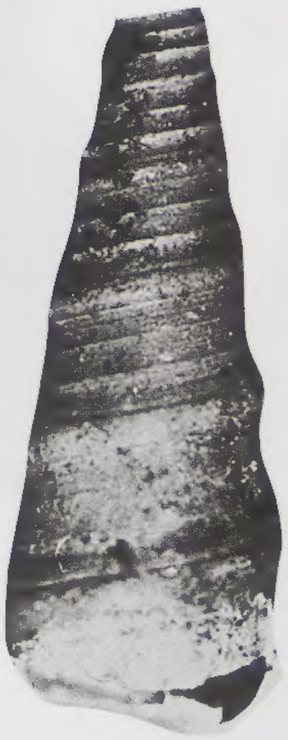

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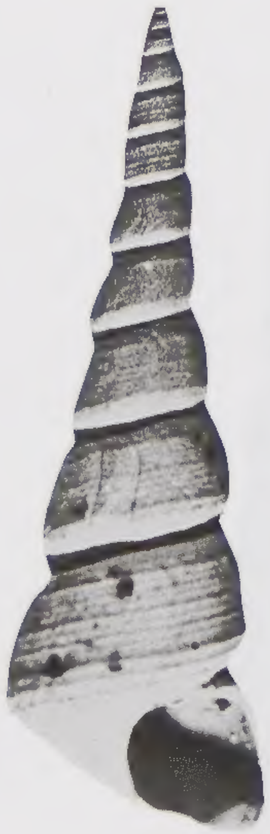

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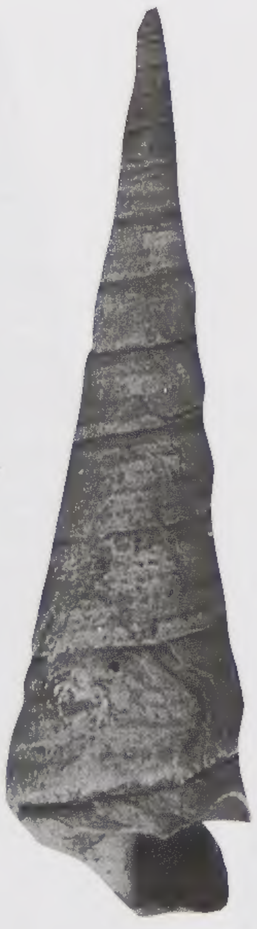

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Figure

1–9. *Haustator perdita* (Conrad). 74

1. MCZIP 29312. Moodys Branch Fm., Locality MS-CL-15. Height = 42.0 mm.
2. MCZIP 29313. Moodys Branch Fm., Locality MS-HN-6. Height = 25.2 mm.
3. *Turritella lowei* Cooke. Holotype USNM 353945. Moodys Branch Fm., Locality MS-HN-4b. Height = 23.0 mm.
4. *Turritella perdita* Conrad. Paralectotype ANSP 13232. Moodys Branch Fm., Locality MS-HN-1. Height = 37.7 mm.
5. *Turritella perdita* Conrad. Paralectotype ANSP 13232. Moodys Branch Fm., Locality MS-HN-1. Height = 35.0 mm.
6. Scanning electron micrograph of damaged apex, showing initiation of spiral sculpture. MCZIP 29340, Locality MS-CL-15. ×150.
7. Scanning electron micrograph of apex. USNM specimen. USGS 1466. Moodys Branch Fm., Locality MS-HN-4.
8. Scanning electron micrograph of apex. MCZIP 29342d. Moodys Branch Fm., Locality MS-CL-15. ×28.
9. Scanning electron micrograph of apex showing initiation of spiral sculpture. MCZIP 29341a. Moodys Branch Fm., Locality MS-HN-6. ×110.

10. *Haustator infans* (Stenzel and Turner). Syntype TMM/TBEG 20957. Stone City Beds, Locality TX-BU-1. Height = 9.0 mm. . . . 73

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1–11. *Haustator carinata* (I.Lea) 68

1. *Turritella carinata* I.Lea. Syntype ANSP 5662. Gosport Sand, Locality AL-MO-1a. Height = 28.1 mm.
2. *Turritella carinata* I.Lea. Lectotype ANSP 5661. Gosport Sand, Locality AL-MO-1a. Height = 27.9 mm.
3. *Turritella carinata* I.Lea. Hypotype PRI 2893. Gosport Sand, Locality AL-MO-1a. Height = 48.0 mm.
4. MCZIP 29293. Gosport Sand, Locality AL-WA-6. Height = 48.5 mm.
5. MCZIP 29292. Gosport Sand, Locality AL-CL-4. Height = 36.9 mm.
6. MCZIP 29294. Gosport Sand, Locality AL-MO-1a. Height = 43.9 mm.
7. *Turritella carinata* I.Lea. Hypotype USNM 497995. Gosport Sand, Locality AL-MO-1a. Height = 39.5 mm.
8. Scanning electron micrograph of apex. MCZIP 29339a. Gosport Sand, Locality AL-MO-1a. ×24.
9. Scanning electron micrograph of damaged apex showing initiation of spiral sculpture. Same specimen as Figure 8. ×160
10. *Turritella carinata palmerae* Bowles. Holotype USNM 497997. Lisbon Fm., Locality AL-MO-4. Height = 29.0 mm.
11. MCZIP 29295. Gosport Sand, Locality AL-CL-4. Height = 35.6 mm.

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1,4,5. *Haustator rina* (Palmer). 76
1. MCZIP 29335. Upper Lisbon Fm., Locality AL-MO-1b. Height = 50.2 mm.
4. Scanning electron micrograph of apex and early teleoconch whorls. MCZIP 29336. Lisbon Fm., Locality AL-CL-14. ×14
5. Scanning electron micrograph of broken apex showing initiation of spiral sculpture. Same specimen as Figure 4. ×150

2. *Haustator subrina* (Palmer). MCZIP 29304. Upper Lisbon Fm., Locality AL-MO-1b. Height = 58.7 mm. 78

3. *Haustator rivurbana* (Cooke). Unnumbered MGS specimen. Moodys Branch Fm., Locality MS-HN-3. Height = 30.3 mm. 78

6–8. *Turritella exoleta* (Linnaeus). 26
6. Unnumbered specimen in the collection of the Rijksmuseum van Natuurlijke Historie, Leiden. Recent. Guyana Shelf. Height = 46.7 mm.
7. Scanning electron micrograph of apex. MCZIP 29337. Recent. Gulf of Mexico. ×20.
8. Scanning electron micrograph of apex showing initiation of spiral sculpture. MCZIP 29338. Recent. Gulf of Mexico. ×60.

9. *Haustator cortezi* (Bowles). 70
Holotype USNM 495172. Cook Mountain Fm., Locality MX-TA-1. Height = 30.0 mm (from Stenzel and Turner, 1942).

10. *Haustator fischeri* (Palmer). 72
FLMNH 5411. Inglis Fm., Levy County, Florida. Height = 19.6 mm.

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1. *"Turritella" plummeri* Stenzel and Turner. Holotype FMNH-UC 57373. Kincaid Fm., Locality TX-KA-7. Height = 36.5 mm. . 37
2. *"Turritella" ola* Plummer. Holotype FMNH-UC 31281. Kincaid Fm., Locality TX-KA-7. Height = 36.0 mm. 37
3. *"Turritella" kincaidensis* Plummer. Lectotype FMNH-UC 31280. Kincaid Fm., Locality TX-KA-5. Height = 25.0 mm. 37
4. *Palmerella levicunea* (Harris). MCZIP 29277. Porters Creek Fm., Matthews Landing Marl Mbr., Locality AL-WI-3. Height = 37.6 mm. 53
5. *Palmerella* sp. MCZIP 29280a. Nanjemoy Fm., Woodstock Mbr., Locality VA-HA-3. Height = 20.7 mm. 66
6. *"Turritella" polysticha* Stenzel and Turner. FMNH-UC 57371. Wills Point Fm., Solomon Branch Mbr., Locality TX-BA-34. Height of largest specimen = 12.2 mm. 37
7. *"Turritella" saffordi* Gabb. MCZIP 29289. Clayton Fm., Locality MS-TI-8. Height = 32 mm. Latex cast. 37
8. *Palmerella hilli* (Gardner). Holotype USNM 373054. Kincaid Fm., Locality TX-BA-2b. Height = 35.9 mm. 52
9,10. *Palmerella stenzeli* new species. 66
   9. Holotype MCZIP 29270. Kincaid Fm., Tehuacana Limestone Mbr., Locality TX-KA-5. Height = 33.4 mm.
   10. Paratype MCZIP 29273. Kincaid Fm., Tehuacana Limestone Mbr., Locality TX-KA-5. Height = 44 mm.

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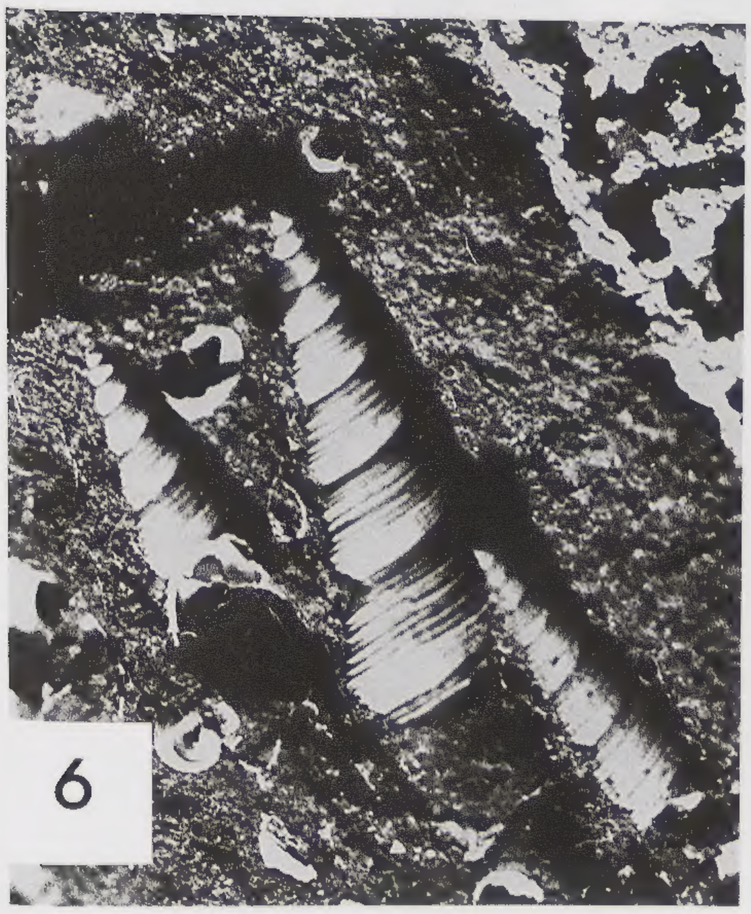

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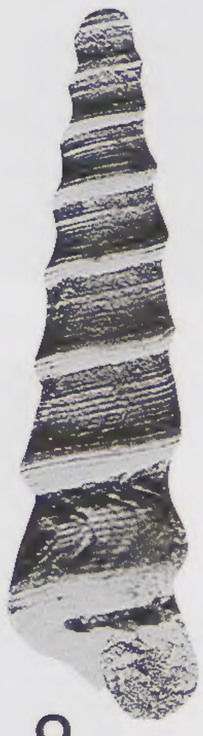

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EXPLANATION OF PLATE 12

Figure — Page

1–4. *"Turritella" aldrichi* Bowles. 81

1. Scanning electron micrograph of apex, showing protoconch and initiation of spiral sculpture. MCZIP 29333a. Porters Creek Fm., Matthews Landing Marl Mbr., Locality AL-WI-3. ×140.
2. Scanning electron micrograph of apex and early teleoconch whorls. MCZIP 29334a. Porters Creek Fm., Matthews Landing Marl Mbr., Locality AL-WI-3. ×14.
3. MCZIP 29305. Porters Creek Fm., Matthews Landing Marl Mbr., Locality AL-WI-3. Height = 38.8 mm.
4. *Turritella aldrichi* Bowles. Paratype USNM 495149. Porters Creek Fm., Matthews Landing Marl Mbr., Locality AL-WI-3. Height = 41.0 mm.

5, 9–11. *"Turritella" multilira* Whitfield. 85

5. Syntype FMNH-UC 24521. Nanafalia Fm., Locality AL-MA-1? Height = 43.5 mm.
9. MCZIP 29334a. Tuscahoma Fm., Bells Landing Marl Mbr., Locality AL-MO-3. Height=47.3 mm.
10. MCZIP 29334b. Tuscahoma Fm., Bells Landing Marl Mbr., Locality AL-MO-3. Height=45.8 mm.
11. Unnumbered GSA specimen. Nanafalia Fm., Locality AL-MA-1. Height = 105.9 mm.

6,7. *"Turritella" toulmini,* new species. 90

6. Plastoparatype MCZIP 29276. Clayton Fm., Locality AL-BA-1. Height = 56.6 mm.
7. Paratype MCZIP 29283. Clayton Fm., Locality AL-BA-1. Height = 32.9 mm.

8. *"Turritella" claytonensis* Bowles. Holotype USNM 131637. Clayton Fm., Locality AL-WI-9. Height = 68 mm. (from Stenzel and Turner, 1942). 82

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1–4. *"Turritella" humerosa* Conrad. 84

1. Paratype ANSP 31388. Aquia Fm., Locality MD-PG-6. Height = 90.2 mm.
2. Lectotype ANSP 31388. Aquia Fm., Locality MD-PG-6. Height = 89.6 mm.
3. Scanning electron micrograph of broken apex showing early teleoconch sculpture. MCZIP 29332. Aquia Fm., Locality VA-ST-4. ×240.
4. Scanning electron micrograph of broken apex. Same specimen as Figure 3. ×80.

5. "*Turritella*" sp. ("*prehumerosa*" Govoni, 1983). Paratype, unnumbered USNM specimen. Brightseat Fm., Locality MD-PG-12. Height = 29.6 mm. 88

6–8. *"Turritella" eurynome* Whitfield. 83

6. Syntype FMNH-UC 24505. Tuscahoma Fm., Bells Landing Marl Mbr. ?, Locality AL-MO-3 ? Height = 27.5 mm.
7. Unnumbered GSA specimen. Tuscahoma Fm., Bells Landing Marl Mbr., Locality AL-MO-3. Height = 86.4 mm.
8. *Turritella bellifera* Aldrich. Holotype USNM 644614. Tuscahoma Fm., Bells Landing Marl Mbr., Locality AL-MO-3. Height = 85.0 mm.

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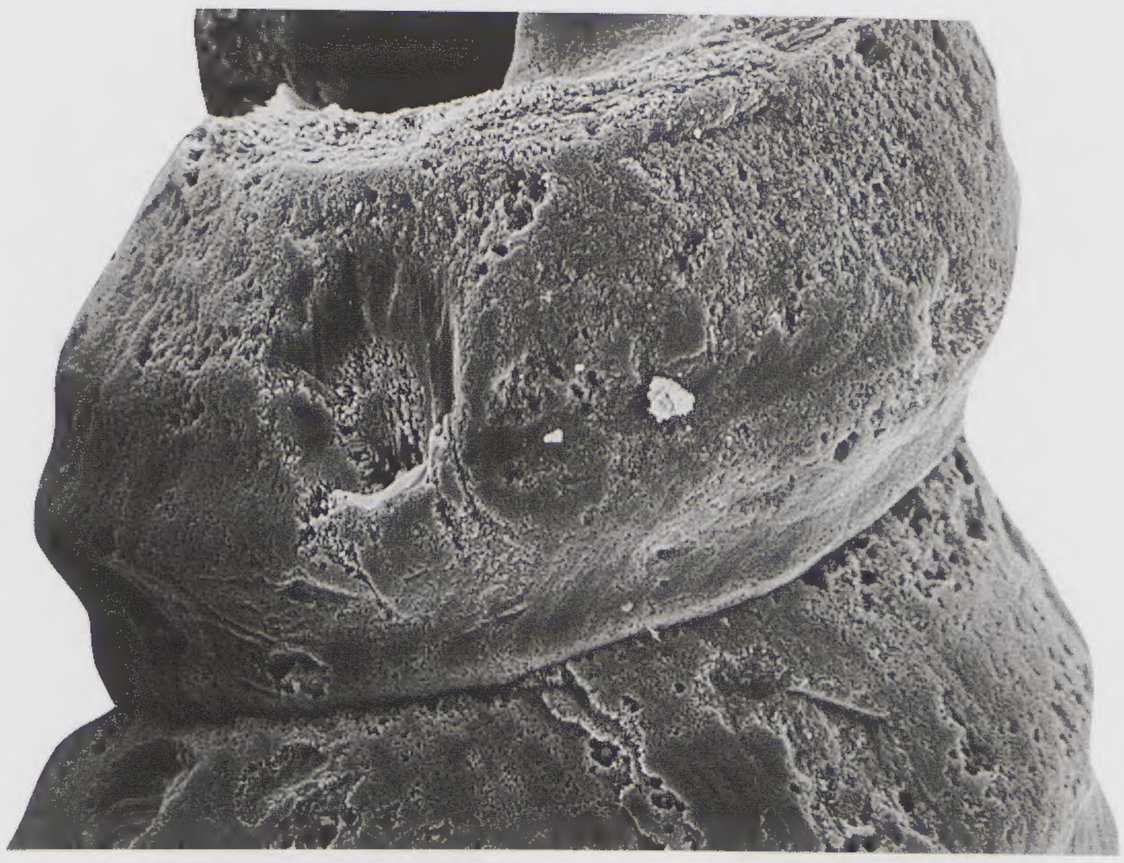

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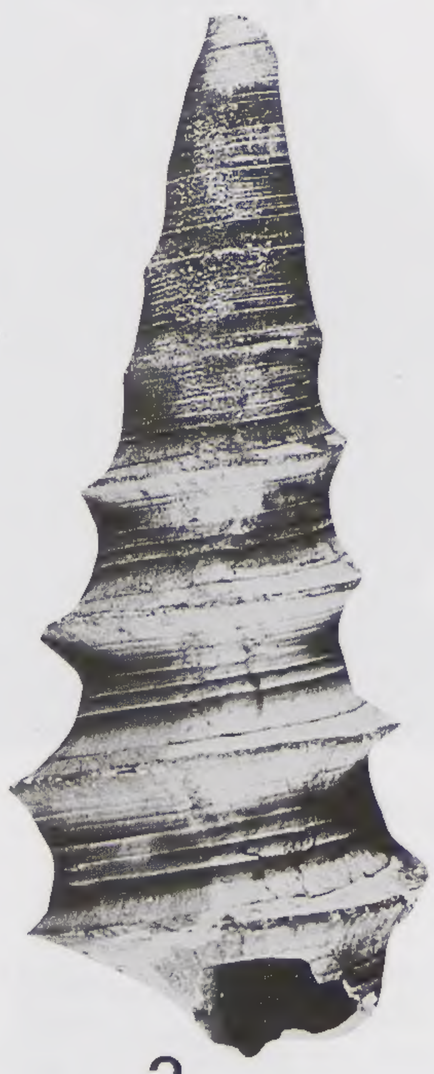

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1–4,6. *"Turritella" praecincta* Conrad. 86

1. *"Turritella" praecincta praecincta.* USNM 559308. Tuscahoma Fm., Greggs Landing Marl Mbr. Locality AL-MO-5. Height = 76.0 mm.
2. *"Turritella" praecincta praecincta.* MCZIP 29349. Tuscahoma Fm., Bells Landing Marl Mbr., Locality AL-MO-3. Height = 67.7 mm.
3. *"Turritella" praecincta praecincta.* MCZIP 29280. Tuscahoma Fm., Bells Landing Marl Mbr., Locality AL-MO-3. Height = 98.3 mm. Note double carina.
4. *"Turritella" praecincta virginiensis* n. ssp. Holotype MCZIP 29093. Aquia Fm., Locality VA-KG-5. Height = 48.3 mm.
6. *"Turritella" praecincta virginiensis.* MCZIP 29330. Black Mingo Group, Williamsburg Fm., Locality SC-BE-3. Height = 48 mm. Latex cast made from specimen in collection of USGS.

5. *"Turritella" biboraensis* Gardner. Holotype USNM 370989. Kincaid Fm., Locality TX-MV-1. Height = 42.4 mm. (from Stenzel and Turner, 1942) 82
7. *"Turritella" nasuta* Gabb. MCZIP 29318. Lisbon Fm., Locality AL-MO-1b. Height = 41.3 mm. 37

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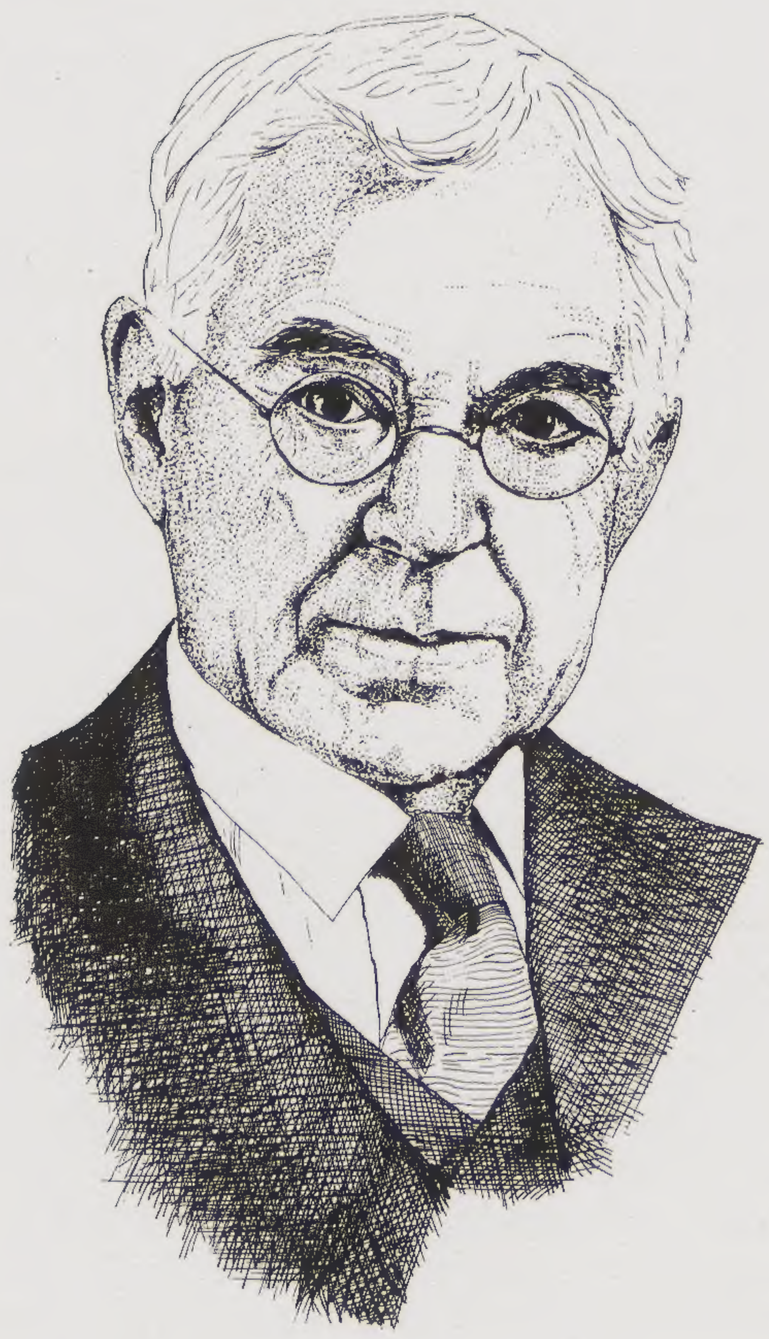

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(1864 - 1952)

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